HEREDITY

BY THE SAME AUTHOR

THE STUDY OF ANIMAL LIFE

An authoritative and thoroughly comprehensive exposition by a leading authority on the study of Zoology and Natural History. New and Revised Edition. With many Illustrations.

HEREDITY

BY J. ARTHUR THOMSON, M.A., LL.D.

Regius Professor of Natural History in the University of Aberdeen

AUTHOR OF "THE STUDY OF ANIMAL LIFE," "THE SCIENCE OF LIFE," "OUTLINES OF ZOOLOGY," ETC.

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I DEDICATE THIS BOOK

WITH THEIR KIND PERMISSION

TO

FRANCIS GALTON AND AUGUST WEISMANN

WHOSE

MAGISTRAL STUDIES ON HEREDITY

HAVE MADE US ALL THEIR DEBTORS

PREFACE TO THIRD EDITION

This book, originally published in 1907, is intended as an introduction to the study of heredity, a subject of fascinating interest and of great practical importance. In recent years much progress has been made in the scientific study of heredity, and, as the literature is widely scattered and often very technical, there may be utility in an exposition which aims at being comprehensive and accurate, and yet relatively simple. The bibliography will enable serious students to fill in details, and follow up clues. It is arranged with a subject-index, so that the literature dealing with particular points can be seen at a glance.

The book has aimed at a fair-minded treatment of the numerous debatable questions, for it is too soon to settle down to fixed conclusions on more than a few points. An attempt has been made to keep practical problems in view, but it has not been found advisable to risk many concrete suggestions. In most cases we do not as yet know or understand enough to warrant more than a general recommendation to take thought for the morrow by considering the ideal of Eugenics.

A glance at the book will show that prominence has been

given to three kinds of conclusions—those reached by microscopic study of the germ-cells, those reached by the application of statistical methods, and those reached through experiment. There is equal justification for these three ways of attacking the mysterious problems, and the results which have been reached in a few years by a relatively small number of resolute investigators, deserve the attention of all thoughtful men and women. The new facts are of especial interest to medical practitioners, to educationists, including clergymen, to social reformers, and to actual or prospective parents.

I have, throughout, acknowledged my indebtedness to authorities; and the bibliography (which is merely representative) shows how many fields there are from which to glean. In particular, I have been indebted to the works of Galton, Weismann, Pearson, Bateson, and De Vries.

I have to thank my friends Mr. E. S. Russell and Dr. John Rennie for going over the proofs of the first edition, and saving the pages from many mistakes. Dr. Leslie Mackenzie was kind enough to read the chapter on Heredity and Disease, and some of his helpful suggestions have been incorporated. I have to thank Professor C. Correns and Professor H. E. Ziegler for generously allowing me to copy four admirable diagrams; also Mr. Young Pentland and the Walter Scott Publishing Company for allowing me the use of a number of figures which have done duty in other books of mine. My thanks are also due to Mr. Murray, who has encouraged me in a work which I was often attempted to abandon, whose good-humoured patience over many delays I should long since have exhausted had he been as many men are.

The demand for a third edition has given me the opportunity

of correcting some errors—for a knowledge of which I am in part indebted to my critics—and of inserting references to some of the new discoveries that have been recently made in this rapidly progressive department of Biology.

J. A. T.

THE UNIVERSITY OF ABERDEEN,
January 1919.

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HEREDITY

CHAPTER I

HEREDITY AND INHERITANCE: DEFINED AND ILLUSTRATED

§ 1. *Importance of the Study of Heredity.*
§ 2. *What the Terms Mean.*
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§ 1. *Importance of the Study of Heredity*

Heredity determines the Individual Life.—There are no scientific problems of greater human interest than those of Heredity—that is to say, the genetic relation between successive generations. Since the issues of the individual life are in great part determined by what the living creature is or has to start with, in virtue of its hereditary relation to parents and ancestors, we cannot disregard the facts of heredity in our interpretation of the past, our conduct in the present, or our forecasting of the future. Great importance undoubtedly attaches to Environ-

ment in the widest sense,—food, climate, housing, scenery, and the animate *milieu*; and to Function in the widest sense,—exercise, education, occupation, or the lack of these; but all these potent influences act upon an organism whose fundamental nature is determined, though not rigidly fixed, by its Heredity—that is, we repeat, by its genetic relation to its forebears. As Herbert Spencer said, "Inherited constitution must ever be the chief factor in determining character"; as Disraeli said, more epigrammatically and less correctly, "Race is everything."

Heredity is a Condition of all Organic Evolution.—In the same way, when we consider the race rather than the individual, we must admit that in so far as evolution depends on inborn organic changes, on what is bred in the bone and imbued in the blood, as distinguished from individual efforts and acquirements, external institutions and traditional culture, it is conditioned by the hereditary relation which binds one generation to another. Heredity is a *condition* of all organic evolution. Innate changes or variations, which form the raw material of constitutional progress or degeneracy, have direct racial importance because they are certainly transmissible; while, on the other hand, bodily modifications or acquired characters, due to changes in environment or in function, probably have no *direct* racial importance, since there is little or no evidence that they are ever hereditarily entailed. They are individually important, and in human society they are of much moment, but if they are not transmissible they do not take organic grip, and they cannot afford material for selection to work with. For the human race, the external heritage of tradition, institutions, and law, the permanent products of literature and art, the registrated results of science, and so on, are of paramount importance, but they are outside the immediate problem of organic or natural inheritance. As far as the slow, sure process of constitutional or organic evolution is concerned, everything depends on the heritable resemblances and the heritable variations which form

the material on which the many diverse forms of selection and isolation operate.

In olden days thoughtful men seemed to see the threads of life within the hands of three sister Fates,—of one who held the distaff, of another who offered flowers, and of a third who bore the abhorred shears of death. So, in Scandinavia, the young child was visited by three sister Norns, who brought characteristic gifts of the past, the present, and the future, which ruled the life to be as surely as did the hands of the three Fates. So, too, in days of scientific enlightenment, we still think of Fates and Norns, though our conceptions and terms are very different. What the living creature is or has to start with in virtue of its hereditary relation; what it does in the course of its activity; what surrounding influences play upon it,—these are the three determining factors of life. Heredity, function, and environment—*famille, travail, lieu*—are the three sides of the biological prism, by which, scientifically, we seek to analyse the light of life, never forgetting that there may be other components which we cannot deal with scientifically, just as there are rays of light which our eyes can never see.

In novels like Zola's *Dr. Pascal,* in plays like Ibsen's *Ghosts,* in sermons and newspaper articles, in large books and health lectures, in season and out of season, we have all heard in the last few years much about the importance of heredity; and though it is to be feared that many widespread impressions on the subject are misleading, the awakening of keen interest is in itself a symptom of progress. What is now required is a serious study of what has been securely established. Otherwise we shall continue to think in platitudes and act on guesses.

Practical Importance to Breeders and Cultivators.—And what is important in regard to Man's heredity is even more demonstrably important in regard to his domesticated animals and cultivated plants. What has been achieved in the past in regard to horses and cattle, pigeons and poultry, cereals and

chrysanthemums, by experimental cleverness and infinite patience, may be surpassed in the future if breeders and cultivators can attain to a better understanding of the more or less obscure laws of inheritance on which all their results depend.

Importance in Biological Theory.—The study of heredity is also of fundamental importance in the domain of pure science, in the biologist's attempt to interpret the process of evolution by which the complexities of our present-day fauna and flora have gradually arisen from simpler antecedents. For heredity is obviously one of the *conditions* of evolution,—of continuance as well as of progress. There would have been heredity even if there had been a monotonous world of Protists without any evolution at all, but there could not have been any evolution in the animate world without heredity as one of its conditions. The study of heredity is inextricably bound up with the problems of development, reproduction, fertilisation, variation, and so on; in short, it is one of the central themes of Biology.

§ 2. *What the Terms Mean*

The Terms are tinged with Metaphor.—In the popular, if not also in the biological mind, there often lurks the idea of a hypothetical agent possessing the organism and uniting the congeries of its characters. Expressed in diverse ways, there is a prevalent conception of an organismal unity which gives coherence to the sum of qualities (see Sandeman, 1896). Especially in reference to higher animals with a rich mental life, many find it impossible not to think of a "soul" or "self" to which the body *belongs*. Naturally enough, therefore, the reappearance in the offspring of qualities which characterised its parents or its ancestors has been persistently likened to the inheritance of a legacy. But this is to some extent a metaphorical expression, and not without its dangers.

At first the Organism and the Inheritance are Identical.—A

moment's consideration suffices to show that ideas and phrases borrowed from the inheritance of property—something quite apart from the individual who inherits—are apt to cause obscurity and fallacy when applied to the inheritance of characters which literally constitute the organism and are inseparable from it. Therefore, as the biological conception of inheritance seems still to suffer from the irrelevancy of the analogy to which

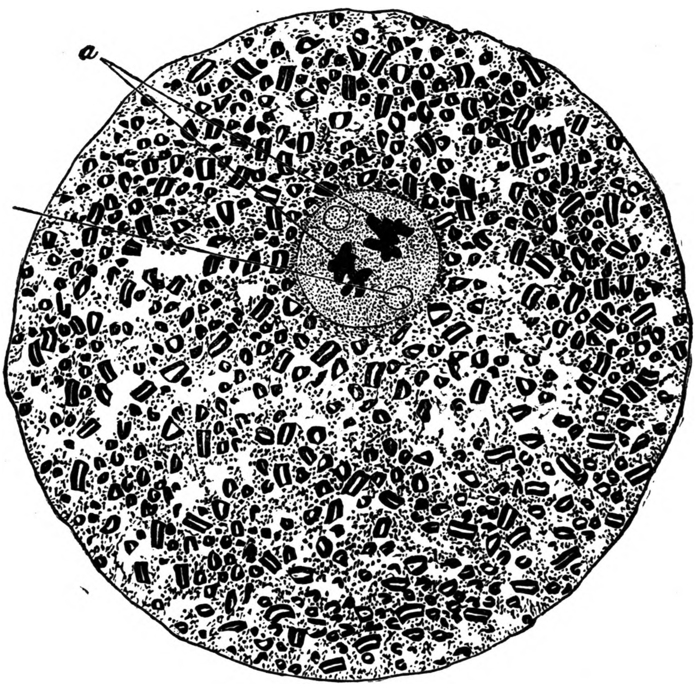

FIG. 1.—Ovum of a threadworm (*Ascaris*), showing (*a*) the chromosomes of the nucleus, and the reserve products in the surrounding cell-substance.—From Carnoy.

the term owes its origin, let us dwell for a little on the fact that, at the start of an individual life, the inheritance and the organism are identical. In other words, the idea of organic inheritance is merely a convenient scientific abstraction, by which we seek to distinguish what the organism is, in virtue of its germinal origin, from what it is as the result of the influence of ensuing circumstances. If we may use Galton's and Shakespeare's terms, the idea of organic inheritance is an abstraction by which

we seek to distinguish what is due to "Nature" from what is due to "Nurture."

Heredity and Inheritance defined.—In regard to property there is a clear distinction between the heir and the estate which he inherits, but at the beginning of an individual life we cannot biologically draw any such distinction. The organism and its inheritance are, *to begin with,* one and the same. It is easy to make this clear. Every living creature arises from a parent or from parents more or less like itself; this reproductive or genetic relation has a visible material basis in the germinal matter (usually egg-cell and sperm-cell) liberated from the parental body or bodies; by inheritance we mean all the qualities or characters which have their initial seat, their physical basis, in the fertilised egg-cell; the expression of this inheritance in development results in the organism. Thus, heredity is no entity, no force, no principle, but a convenient term for *the genetic relation between successive generations,* and inheritance includes *all that the organism is or has to start with in virtue of its hereditary relation.*

Nature and Nurture.—The fertilised egg-cell implicitly contains, in some way which we cannot image, the potentiality of an adult creature,—a tree, a daisy, a horse, a man. If this potentiality is to be realised there must be an appropriate environment, supplying food and oxygen and liberating-stimuli of many kinds. Surrounding influences—maternal or external—begin to play upon the developing germ, and without these influences the inheritance could not be expressed, the potentialities could not be realised. Thus the organic inheritance implies an environment, apart from which it means nothing and can achieve nothing. Indeed, it is only by an abstraction that we can separate any living creature from an environment in which it can live. Life implies persistent action and reaction between organism and environment.

But while the inherited nature and its possibilities of action

and reaction must be regarded as rigorously determined by the parental and ancestral contributions, the nurture—the environmental influences—must not be thought of as pre-determined. In fact, the surrounding influences are very variable, and the nature of the young organism may be profoundly changed by them. Thus, we soon find it possible to distinguish between the main features, which are the normal realisations of the inheritance in a normal environment, and peculiarities which are due to peculiarities in nurture. The characters of a newly-hatched chick stepping out of the imprisoning egg-shell are in the main strictly hereditary; but they need not be altogether so, for during the three weeks before hatching there has been some opportunity for peculiarities in the environment to leave their mark on the developing creature. Still more is this the case with the typical mammalian embryo, which develops often for many months as a sort of internal partner within the mother—in a complex and variable environment. And as life goes on, peculiarities due to nurture continue to be superimposed on the hereditary qualities.

William of Occam's Razor.—Our preliminary attempt to get rid of capitals, to make the terms heredity and inheritance quite objective, is in line with what has occurred in other departments of science. For one of the distinctive features of the nineteenth century has been a reduction in the number of supposed separate powers or entities—the use of William of Occam's razor, in fact. "*Entia non sunt multiplicanda prœter necessitatem.*" "Caloric" was one of the first to be eliminated, yielding to the modern interpretation of heat "as a mode of motion"; "Light" had to follow, when the undulatory or the electro-magnetic theory of its nature was accepted; a specific "Vital Force" is disowned even by the Neo-vitalists; "Force" itself has become a mere measure of motion; and even "Matter" tends to be resolved into units of negative electricity, carrying with them a bound portion of the ether in which they are bathed; and so on. In

view of this progress towards greater precision and simplification of phraseology, it cannot be a matter for surprise that a biologist should affirm that to speak of the "Principle of Heredity" in organisms is like speaking of the "Principle of Horologity" in clocks. The sooner we get rid of such verbiage the better for clear thinking, since heredity is certainly no power, or force, or principle, but a convenient term for the relation of organic or genetic continuity which binds generation to generation. Ancestors, grandparents, parents are real enough; children and children's children are also very real; heredity is a term for the relation of genetic continuity which binds them together. We study it as a relation of resemblances and differences which can be measured or weighed, or in some way computed; as a relation which is sustained by a more or less visible material basis —namely, the germinal matter

§ 3. *Heredity and Inheritance in Relation to other Biological Concepts*

Development.—All living creatures arise from parents more or less like themselves. The reproduction may be *asexual*,—by fission, fragmentation, budding, and similar processes; or *sexual*,—by special germ-cells or gametes, which usually unite in pairs (fertilisation or amphimixis) to start a new individual body. Whatever the *mode of reproduction* may be—and that is a long story by itself—there is a hereditary relation, a genetic continuity. It is the business of the *theory of heredity* to inquire into the precise nature of this genetic relation in the diverse modes of reproduction. In what relation, for instance, does a liberated germ-cell or gamete stand to the body which liberates it? In what relation does a fertilised ovum stand to the germ-cells of the body into which it develops? What contribution does each parent make to the inheritance? Do ancestors also make contributions, and if so, how? To answer this kind of question is the business of *the theory of heredity.*

The separated fragment or the liberated germ-cell has in it the possibility of becoming, in an appropriate environment, a fully-developed organism. Is it possible to form any conception —verifiable or speculative—of the manner in which the inheritance is thus condensed into a fragment or into a germ-cell? Is it possible to picture in any way how the potentialities come to be realised in development; how the obviously complex grows out of the apparently simple? To answer these and similar questions is the business of *the theory of development.*

The facts of *inheritance* are those which rise into prominence when we compare the characters of an organism with those of its parents and its offspring, or when we compare the characters of one generation with those of its predecessors and successors. This is a thoroughly concrete study, for the facts observed are quite independent of any theory of the precise organic relation which binds generation to generation (*the theory of heredity*), and are also quite independent of any theory as to the way in which the germ grows into the adult (*the theory of development*). It is, in the main, an experimental and statistical study.

Before the middle of the nineteenth century considerable attention was given to what may be called the demonstration of the general fact of inheritance—that like tends to beget like. This had, indeed, always been the general opinion of physicians and naturalists, as well as of the laity, but it was a useful task to collect documentary evidence showing that all the inborn characteristics of an organism, whether physical or psychical, normal or abnormal, important or trivial, were *transmissible* to the offspring, if the possibility of having offspring had not been excluded. This task of demonstrating inheritance was well finished by Prosper Lucas, whose large treatise, published in 1847, gave ample evidence for what we now take for granted,— that the present is the child of the past; that our start in life is no haphazard affair, but is rigorously determined by our parentage and ancestry; that all kinds of inborn characteristics may

be transmitted from generation to generation. In short, the fundamental importance of inheritance was long ago demonstrated up to the hilt.

It remains, however, (1) to make the evidence of transmissibility more precise and systematic; (2) to inquire into the transmissibility of subtle characters such as longevity and fecundity; (3) to discover the different degrees of transmissibility, for some characters are much more heritable than others; and (4) to classify different modes of hereditary resemblance—*e.g.* blending of the characters of the two parents, taking after the father in one feature and after the mother in another, apparently resembling one parent only, rehabilitating a grandsire's features, harking back to a remoter ancestor, and so on. What happens when there is close in-breeding or pairing within a narrow radius of relationship? What happens when two hybrids are paired? In what sense, if any, is a disease heritable? These and many similar questions will be discussed in our inquiry into *the facts of inheritance.*

Variation.—Whenever we begin to compare the characters of an organism with those of its parents, we discover that the familiar saying, "Like begets like," must be modified into, "Like tends to beget like." On the one hand, the child is like its parents, "a chip of the old block," a literal *reproduction*; on the other hand, the child is something original, a new pattern, a fresh start—leading the race. We do not gather grapes of thorns, or figs of thistles; yet two brothers may be very unlike one another or either of their parents, and even the peas in one pod may be different. On the one hand, there is a tendency towards continuity, towards persistence of characters, towards complete hereditary resemblance—in short, a kind of organic inertia in a family or stock or species. On the other hand, there is a tendency towards variation, towards new departures, towards incomplete hereditary resemblance, or much more than that. It is necessary to hold the balance between these two

sets of facts, both expressions of the hereditary relation,—inertia, persistence, continuity, resemblances, on the one hand; deviation, novelty, differences, on the other.

Can we hope to discriminate an *apparent* difference between parent and offspring, which is really due to an incompleteness in the expression of the inheritance, from a *real* difference, which is due to the dropping out of an old hereditary item or the addition of a new one? Can we distinguish between inborn peculiarities—germinal variations—and acquired, nurtural peculiarities? Can we distinguish between variations which seem to be simply a little less or a little more of some hereditary character, and variations which involve something new? These and similar questions must be faced in *the study of variation.*

Modifications.—Furthermore, whenever the study of the facts of inheritance becomes critical, it is necessary to try to discriminate between inborn changes, which must have a germinal origin, and are therefore in the strict sense *inherited*, and are liable to be transmitted, and those theoretically quite different changes which are acquired by the body of the individual offspring as the result of peculiarities in function and environment. This is the contrast between *germinal variations* and *bodily modifications*, a contrast which is of fundamental importance in several ways. It is important to try to distinguish resemblances and differences due to inherited nature from resemblances and differences due to nurture. A collier may have his collier father's red hair, and he may also resemble him in having "collier's lung." But while the first resemblance is a fact of inheritance, the second is due to the similarity in their life-conditions. This distinction remains important whatever conclusion be reached in regard to the transmissibility of modifications, but its importance is enhanced when we discover that practically all variations (except sterility) are transmissible, though not always transmitted, and that the evidence of any modification

being transmissible, among multicellular organisms reproducing sexually, is extremely doubtful.

Evolution.—Briefly and concretely stated, the general doctrine of organic evolution suggests, as we all know, that the plants and animals now around us are the results of natural processes of growth and change working throughout unthinkably long ages; that the forms we see are the lineal descendants of ancestors on the whole somewhat simpler; that these are descended from yet simpler forms, and so on, backwards, till we lose our clue in the unknown, but doubtless momentous, vital events of pre-Cambrian ages, or, in other words, in the thick mist of life's beginnings. The essentially simple idea is that the present is the child of the past, and the parent of the future. It is a way of looking at organic history, a genetic description, a modal formulation. A process of Becoming leads to a new phase of Being; the study of evolution is a study of *Werden und Vergehen und Weiter-werden.*

But we have to pass from a modal interpretation to a causal one. We have to try to discover the factors in the age-long process, and this leads us into a region where at present uncertainties abound. As biologists we start with the postulate of simple living organisms—feeding, working, growing, wasting, reproducing in an appropriate environment. And we try to discover the possible factors in the long evolution-process, the outcome of which is the present-day world of life. Amid all the uncertainties, this is certain, that the fundamental condition of evolution is that genetic relation which we call heredity,—a relation such that it admits, on the one hand, of a continuity of hereditary resemblance from generation to generation; and, on the other hand, of an organic changefulness which we call variability. Without the hereditary relation there could have been no succession of generations at all. Without hereditary resemblance on the one hand, and hereditary variation on the other, there could have been no evolution. Any discussion of

the secondary or directive factors which operate upon the raw materials of progress which variability supplies—notably Selection and Isolation—is not relevant at present.

§ 4. *A Question of Words*

In every discussion with a serious purpose it is important that there should be clearness as to the terms used. We must, therefore, ask the reader to notice our definition of the chief terms. Thus by "heredity" we do not mean the general fact of observation that like tends to beget like, nor a power making for continuity or persistence of characters—to be opposed to the power of varying—nor anything but *the organic or genetic relation between successive generations*; and by "inheritance" we mean "organic inheritance"—*all that the organism is or has to start with in virtue of its hereditary relation to parents and ancestors.* We do not forget that for man in particular there is an external heritage—a social inheritance—which counts for much. By innate or inborn we mean all that is potentially implied in the fertilised egg-cell; by the expression of the inheritance we mean the realisation of inborn potentialities in the course of development in an appropriate environment; by a congenital character (*pace* many medical writers) we mean one demonstrable at birth, which is not necessarily germinal, being often due to peculiarities—*e.g.* infection or poisoning or mechanical injury during pre-natal development. Thus, tubercle may be congenital, but it is never inherited. By modifications or acquired characters we mean structural changes in the body induced by changes in the environment or in the function, and such that they transcend the limit of organic elasticity, and therefore persist after the inducing conditions have ceased to operate. By a variation we mean not *any* observed difference between offspring and parent, between an individual and the mean of

the stock in respect of a given character; we mean observed differences minus all bodily modifications, we mean changes which have a germinal origin.

These definitions will become clearer in the course of our exposition. Our present point is to warn the reader against starting on his journey without reading the conditions on the ticket, and to protest against the slackness with which the terms are so often used. A large part of the energy expended on the long-drawn-out controversy as to the transmission of acquired characters or modifications has been wasted through inattention to the precise significance of the technical terms employed.*

To speak of a man "fighting against his heredity" may express a real fact, but it is verbally erroneous. The American's question, "Is my grandfather's environment my heredity?" is an offence against ordinary English as well as against scientific phrasing; it should probably read, "Have the structural changes induced by environmental influences on my grandfather's body had any effect on my inheritance?" Nor can we pardon from an expert such a sentence as this, "I look upon Heredity as an acquired character, the same as form or colour, or sensation is, and not as an original endowment of matter" (Bailey, 1896, p. 23). When the moralist writes: "The only limitations imposed on a man are those which his own nature makes," the biologist asks, "But what is his own nature? Is

* It may be noted that Galton's work on *Natural Inheritance* is rightly so entitled, for it deals mainly with a statistical comparison of the characters of successive generations. Inheritance is also the chief subject of the works of Lucas and Ribot, although these have heredity for their title. Or, to take another example, Weismann's work entitled *The Germ-Plasm, a Theory of Heredity*, is in great part a theory of heredity, but, naturally enough, it is also in great part a theory of development. The German language has the same word, *Vererbung*, for both Heredity and Inheritance. As the English language is rich in related terms, laxity of expression is less excusable. Besides "heredity" and "inheritance" we have "heritage," "transmission," and so on. But to speak of the parent as transmitting is apt to suggest an erroneous idea.

it not the expression of a predetermined inheritance in a more or less predetermined environment ?"

Definitions of "Heredity."—It may be of interest to give a few samples of definitions :

"The word 'Heritage' has a more limited meaning than 'Nature,' or the sum of inborn qualities. Heritage is confined to that which is inherited, while Nature also includes those individual variations that are due to other causes than heredity, and which act before birth."—Francis Galton, *Natural Inheritance*, 1898, p. 293.

"Heredity is the law which accounts for the change of type between parent and offspring, *i.e.* the progression from the racial towards the parental type."—Karl Pearson, *The Grammar of Science*, 1900, p. 474.

"Under heredity we understand the transference to the offspring of qualities of the parent or parents."—T. H. Montgomery, Jr., *Proc. American Phil. Soc.* xliii. 1904, p. 5. [But the line of descent is from germ-cell to germ-cell. The parent is the custodian or trustee of the germ-cells rather than their producer. It is too metaphorical to speak of the "parent transferring qualities to the offspring." The hereditary relation includes the occurrence of variations as well as the reproduction of likenesses. And what are the offspring apart from their inheritance ?]

"'Heredity' is most usually defined by biologists as referring generally to all phenomena covered by the aphorism 'like begets like.' In this sense it denotes, *inter alia*, the phenomenon of the constancy of specific or racial types and of sexual characters ; a character may be said to be *inherited* when it always, in one generation after another, is one of the characters of the species, of the race, or of the one sex of the race, as distinct from the other. The species, race, or sex, so to speak, 'begets its like' as a whole. But then a further question remains ; even if the type of the race is constant, do *individual* types within the race beget their like ? In so far as any *individual* diverges in character from the mean of the race, do his offspring tend to diverge in the same direction, or not ? It is to this question that statisticians have confined themselves, and they speak of a character being 'inherited' or not according as the answer to the question is yes or no—they deal solely with what we may term '*individual* heredity.'"—G. Udney Yule, 1902, p. 196. [Biologists are as much concerned with individual

heredity as statisticians are, indeed more so; statistical results are based on individual data, but they do not admit of individual application.]

"Living matter has the special property of adding to its bulk by taking up the chemical elements which it requires and building up the food so taken as additional living matter. It further has the power of separating from itself minute particles or germs which feed and grow independently and thus multiply their kind. It is a fundamental character of this process of reproduction that the detached or pullulated germ inherits or carries with it from its parents the peculiarities of form and structure of its parent. This is the property known as Heredity. It is most essentially modified by another property—namely, that though eventually growing to be closely like the parent, the germ (especially when it is formed, as is usual, by the fusion of two germs from two separate parents) is never identical in all respects with the parent. It shows Variation. In virtue of Heredity, the new congenital variations shown by a new generation are transmitted to their offspring when in due time they pullulate or produce germs."—E. Ray Lankester, *Kingdom of Man*, 1907, p. 10.

"By inheritance we mean those methods and processes by which the constitution and characteristics of an animal or plant are handed on to its offspring, this transmission of characters being, of course, associated with the fact that the offspring is developed by the processes of growth out of a small fragment detached from the parent organism."—R. H. Lock, *Recent Progress in the Study of Variation, Heredity, and Evolution*, 1906, p. 1.

"Heredity.—The transference of similar characters from one generation of organisms to another, a process effected by means of the germ-cells or gametes."—Lock, *op. cit.* p. 292.

§ 5. *The Problems Illustrated*

Even in ancient times men pondered over the resemblances and differences between children and their parents, and wondered as to the nature of the bond which links generation to generation. But although the problems are old, the precise study of them is altogether modern. The foundations of embryology had to be laid, the nature and origin of the physical basis of inheritance

—the germ-cells—had to be elucidated, the general idea of evolution had to be realised, before the problems of heredity and inheritance could even be stated with precision. Moreover, it seems to have required the experience of many years of "fumbling" before the main body of biologists became convinced that the problems could not be satisfactorily studied in the armchair, nor settled by *a priori* argument. Now, however, it is unanimously agreed that a satisfactory study of heredity and inheritance demands a minute inquiry into the history of the germ-cells, a statistical study of the characters of successive generations, a careful criticism of the older data and of popular impressions, and a testing of hypotheses by experimental breeding. Let us give a few random illustrations in order to show what some of the problems are:

The race-horse Eclipse was the sire of many foals: it is a problem in heredity to compare them with him, and to inquire into the vital arrangements, in virtue of which many of them reproduced his remarkable quality of swiftness. He had also a peculiar, quite useless spot of colour, which reappeared even in the sixth generation of his progeny.

In the ancestry of Kaiser Wilhelm II. there have been four grandparents, eight great-grandparents, fourteen (not 16) great-great-grandparents, twenty-four (not 32) great-great-great-grandparents: it is a problem in heredity to compare the qualities of these successive generations of ancestors, and to inquire if they render more intelligible the doings and sayings of the personality in question.

The assassin of the Empress of Austria is said to have been the child of a dissolute mother and a dipsomaniac father: it is a problem in heredity to inquire whether this parentage may render more intelligible an outrage which made Europe shudder.

A white man of considerable intellectual ability marries a negro woman of great physical beauty and strength; the result

may be—has been—a mulatto who inherits some of his father's intellectual virtue and some of his mother's physical strength, including, for instance, a peculiar insusceptibility to yellow fever. Here are complex problems of inheritance. How is it that certain characteristics of the son are almost wholly of paternal origin, while in other respects he takes after his mother?

An English sheep-dog may show a paternal eye on one side of the head, a maternal eye on the other. A piebald foal may have its mother's hair on some patches, its father's hair on others. Such cases raise the problem of the different modes of hereditary resemblance, of the mosaic-like constitution of an inheritance, and of the various ways in which this may find expression in development.

Given in our British population a thousand fathers six feet high, we can predict with great accuracy the *average* height of their sons. Though we cannot make any prediction as to an individual family, we know that the average height of all the sons of these tall men will be nearer the average height of the total male population than the height of six feet is. We know, however, that the tall do not always beget the tall, nor the small the small; that stature in mankind is a character that blends; and that even among the sons of the thousand fathers we have spoken of, there will be every gradation between the tallest and the smallest. How different this is from stature in pure-bred peas, for if a tall variety of pea be crossed with a dwarf, all the offspring are tall, and among their offspring in turn three-fourths are tall and one-fourth dwarf, but none between the two.

White fowls crossed with black ones often have *white* offspring; black guinea-pigs crossed with white ones have *black* offspring; black-eyed white guinea-pigs crossed with albinos have *black* offspring. It seems at first sight arbitrary, but a rational interpretation of each of these results has been given.

A pair of blue Andalusian fowls of selected breed have chickens. But only about half of these are "blue," the rest are blacks or splashed whites. Why is this? The blacks inbred produce only blacks, the splashed whites produce splashed whites or whites, but if the blacks and splashed whites are paired the progeny is altogether "blue." Why is this?

We read of a mare which, after bearing a foal to a quagga, bore a zebra-striped foal to a horse. Breeders of dogs say that a thoroughbred bitch is spoilt for true breeding if she has once been crossed by a mongrel. Is it possible that a father can influence the subsequent offspring of the same mother by a different father? This is a problem partly in scientific criticism of evidence, but it raises interesting questions regarding the physiology of reproduction and regarding the hereditary relation.

In the sixteenth century Montaigne was puzzled by the fact that, at the age of forty-five, he developed, just like his father, a stone in the bladder. The puzzle of the supposed legacy had its fine point in the fact that his father did not develop his stone till he was sixty-seven years of age, or twenty-five years after Montaigne was born! It is possible that there was here an interesting problem in inheritance; but the likelihood is that it merely illustrated the commonest of phenomena, the inheritance of a constitutional tendency and the repetition of more or less similar habits of life.

Far too much has been made of homochronous heredity!—*i.e.* of the fact that some item in the inheritance may be expressed in the offspring at the same age as in the parents. Thus two brothers, their father, and their maternal grandfather became deaf at the age of forty; blindness occurred in a father and in his four children at the age of twenty-one. But if the constitutions are similar and if the conditions of life are similar, it is not surprising that the expression of an item in the constitution should reach its climax at the same age.

A case is recorded of abnormalities in the fingers traceable

through six generations, and the pathologist Bouchut (cited by Ziegler) refers the origin of the evil to the rage of an ancestor, who terrified his wife during her pregnancy with the wish that the fingers with which she had plucked an apple against his orders might be cut off! Apart from the story's quaint suggestion of a much older episode, it requires but an elementary knowledge of the facts of heredity and inheritance to convince us that the alleged cause was inadequate to account for the effects.

In two hundred families tainted with a predisposition to hæmophilia—an excessive and chronic liability to immoderate hæmorrhage—Grandidier * found six hundred and nine male "bleeders." It is a problem of inheritance (and partly perhaps of sexual physiology) to discover why the disease should be restricted to males; and the interest of the problem is enhanced by the fact that the disease rarely passes from father to son, but *usually* from a male parent, through an apparently *unaffected* daughter, to a grandson. In short, the female offspring of bleeders hand on the taint to male offspring, without themselves showing the disease.†

De Candolle ‡ reported from American statistics that thirty per cent. of the children of congenitally deaf-mute parents were deaf-mute, but that the percentage was fifteen when only one parent was congenitally deaf-mute. It is a problem of heredity to interpret the greater frequency of inheritance when both parents were affected.

While there is much and justifiable uncertainty in regard to the origin of what are called instincts, there is no doubt that an organism's inheritance often includes the power of carrying out a complex series of operations without experience and without education when the appropriate stimuli occur.

* Grandidier, *Die Hæmophilie* (1876).

† Bulloch and Fildes, *Hæmophilia. Treasury of Inheritance*, Pt. xiva. (1911).

‡ De Candolle, *Arch. Sci. Phys. Nat.* xv. p. 25, cited by Ziegler (1886).

Simple illustrations are afforded by instinctive likes and dislikes, attractions and repulsions. "So old is the feud between the cat and the dog," says Spalding, "that the kitten knows its enemy before it is able to see him, and when its fear can in no way serve it. One day, after fondling my dog, I put my hand into a basket containing four blind kittens three days old. The smell that my hand carried with it set them puffing and spitting in a most comical fashion."

Experiments with young birds hatched from artificially incubated eggs and kept away from all contact with their kind show conclusively that certain capacities are truly part of the inheritance, and require no experience or suggestion, while others not more complex require to be learnt. Thus the power of uttering the characteristic call-note is inborn, but chicks require to learn what is good for eating and what is deleterious. Thus the power of executing the proper swimming and diving movements is inherited, but chicks do not instinctively know that water is drinkable. It is one of the problems of inheritance to distinguish between inborn capacities and those which require education.

An even more difficult problem, which Prof. Pearson has successfully tackled by an ingenious indirect method, relates to the inheritance of man's mental and moral qualities. Though very plastic, there is no doubt that they are inherited in rudiment, just like physical characters. Just as the Romans distinguished physically the long-nosed Nasones, the thick-lipped Labeones, the swollen-cheeked Buccones, and the big-headed Capitones, so, as Voltaire points out, "the Appii were ever proud and inflexible, and the Catos always austere."

The literature of inheritance is crowded with examples of the transmissibility of what we cannot but call trivial peculiarities, though the probability is that they are often the correlates of what is important. A few illustrations may be selected :

"A gentleman had a peculiar formation of the right eyebrow.

It was strongly arched, and some of the hairs in the centre grew upwards. Three of his sons have the same peculiarity; one of his grandsons has it also; so has his great-granddaughter, and, if we are to believe the artists, this gentleman's grandfather and great-grandfather had the same peculiarity" (R. W. Felkin).

"There was a family in France, of whom the leading representative could when a youth pitch several books from his head by the movement of the scalp alone. His father, uncle, grandfather, and his three children possessed the same power to the same unusual degree. This family became divided eight generations ago into two branches, so that the head of the above-named branch was cousin in the seventh degree to the head of the other branch. This distant cousin resided in another part of France, and on being asked whether he possessed the same faculty, immediately exhibited his power."

A woman with blonde hair, a birth-mark under the left eye, and a lisp, married a man with dark hair and normal utterance. There were nineteen children, none of whom showed any of the mother's characters. Nor among the numerous grandchildren was there any trace. In the third generation, however, there was a girl with blonde hair, a mark below the left eye, and a lisp.

Girou tells of a man who had the peculiar habit of always sleeping on his back with his right leg crossed over his left. His daughter showed the same habit almost from infancy, and persisted in it in spite of efforts made to make her sleep in an orthodox position. Darwin gives an even better case where a very peculiar gesture reappeared; and there seems no doubt that trivial peculiarities, *e.g.* playing with a lock of hair and idiosyncrasies of handwriting, may reappear even in cases where imitation was out of the question (Büchner, 1882, p. 42).

And thus the list may be followed till we end with evidence of the inheritance of minutiæ often of a most trivial character. Thus: "Schook relates the case of a family nearly all the mem-

bers of which could not endure the smell of cheese, and some of them were thrown into convulsions by it" (R. W. Felkin). Here again we are forced back to the general thesis that the germinal organisation is a coherent individualised unity, which may find similar expression in the most detailed peculiarities of the body.

§ 6. *Denials of Inheritance*

The resemblance between offspring and their parents, both in general and in particular, as to abnormal as well as normal characteristics, cannot be denied as a fact, but it has often been denied *as the result of transmission.* Although the denials, which have varied greatly in degree and motive, are for the most part due to misunderstanding, they may deserve brief consideration, since even to-day we sometimes hear cultured men declaring that "they do not believe in heredity."

The extreme position may be represented by Wollaston, a scientific philosopher of the end of the eighteenth century, who sought to conserve the integrity and sanctity of the human spirit by altogether denying transmission. Each new life was to his mind a fresh start, unrelated in any real sense to parents or ancestors.

The speculative naturalist Bonnet and many others admitted the inheritance of generic and specific characters, but denied that of *individual* characteristics.

Buckle is the most illustrious example of those who, while admitting the inheritance of bodily characters, firmly deny that the same is true in regard to the mind. Buckle maintained that the ordinary method of demonstrating the inheritance of talents by collecting examples of similar mental peculiarities in father and son is in the highest degree illogical; it neglects, for instance, the frequency of coincidence, and yet more the results of similar upbringing and environment.

A consideration of these denials, which have ceased to appeal to many, may be of use as affording opportunity for emphasising two facts.

1. Reappearance of a character from generation to generation does not of itself prove the inheritance of that character, *if* it be originally interpretable as the result of nurture (influences of activity and surroundings operative on the body), and *if* there be from generation to generation a persistence of the conditions which were originally instrumental in evoking the character. It is plain that the reappearance may be the result of similar effects hammered on each successive generation.

Alpine plants brought to a lowland garden have been known to become much changed, and their descendants likewise. But there is good reason to believe, as we shall afterwards see, that the novel conditions directly impressed their effects on each successive crop.

What impressed Buckle was the power of the environment in the widest sense; it holds the organism in its grip, and hammers it into shape. This no one will gainsay, but we know that similar nurture has different results on different natures; the duckling is not known to be less a duckling because hatched and brought up by a hen. Moreover, we know of the reappearance from generation to generation of many characteristics which cannot be interpreted as due to nurture—which often emerge, indeed, in the very teeth of nurture.

At the same time, it is of great importance to bear in mind that an organism cannot be separated from its environment except at the risk of some fallacy. We may say that along with the organic heritage contained in the germ-cells every organism has what may be called an external heritage of appropriate environmental influences, which supply the stimuli for normal development.

Appropriate food is part of the normal environment, and the supply of oxygen and water may be grouped in the same set; other factors, like the osmotic pressure or the presence of calcium salts in

the water, are conditions of embryonic coherence; others, like light and heat, serve to accelerate or to inhibit. It seems, also, that particular combinations of factors are required as the "liberating stimuli" of particular characters in the developing organism. Development is the expression of the inheritance, and the fullness of the expression depends on there being a normal environment. What is called a hereditary defect may be simply a defect in expression due to inadequate environment.

How fundamental the germinal nature is may be realised if we think of Heape's experiment of transferring the fertilised ovum of a long-haired white angora rabbit into another variety of rabbit—a short-coated gray Belgian hare. The young were not less long-haired or less white because of the transplantation of the ova. Similarly Castle and Phillips removed the ovaries from a white albino guinea-pig, inserted those of a young black individual, and had the grafted animal mated with a male albino. Normal albinos mated together always have albino young, but the animal experimented on had to the albino male three litters (six young) all black. The foster-body did not count.

2. Beneath the misunderstanding which has led some to deny the facts of inheritance there is, as we have seen, a reasonable though exaggerated recognition of the potency of similar function and environment in producing resemblance; and there is, perhaps, the recognition of another fact—that of variation. For several reasons—for instance, because the new life usually springs from a fertilised ovum which combines maternal and paternal contributions—the child is never quite like its parents. In other words, we suppose that the germinal material from which a child develops is *not quite the same* as that from which the parents developed, or not quite the same as that from which its brothers and sisters developed, and the result is variation in the true sense. Each offspring has its individuality and is a new creation. Even within a family no two are alike, especially to the careful parent's eye, though the impartial onlooker may be struck by the monotony. On the one hand, "*Alle Gestalten sind ähnlich*"; on the other, "*Keine gleichet der andern.*"

CHAPTER II

THE PHYSICAL BASIS OF INHERITANCE

"Gebt mir Materie, und ich will daraus eine Welt schaffen."—KANT.

"We may regard the nucleus of the cell as the principal organ of inheritance" (a prophecy proved true).—HAECKEL, *Generelle Morphologie*, 1866, vol. i. p. 288.

"The cell is not only the seat of vital activity, but is also the vehicle of hereditary transmission; and the life of successive generations of living beings shows no breach of continuity, but forms a continuous vital stream in which, as Virchow said, rules an 'eternal law of continuity.'"—WILSON, 1900, p. 76.

§ 1. *What is true in the Great Majority of Cases.*

§ 2. *Diverse Modes of Reproduction.*

§ 3. *The Hereditary Relation in Unicellular Organisms.*

§ 4. *The Hereditary Relation in the Asexual Multiplication of Multicellular Organisms.*

§ 5. *Nature and Origin of the Germ-cells.*

§ 6. *Maturation of the Germ-cells.*

§ 7. *Amphimixis and the Dual Nature of Inheritance in Sexual Reproduction.*

§ 8. *Inheritance in Parthenogenesis.*

§ 9. *Wherein the Physical Basis precisely consists.*

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§ 1. *What is true in the Great Majority of Cases*

The Inheritance is usually carried by the Germ-cells.—What was for so long quite hidden from inquiring minds, or but dimly discerned by a few, is now one of the most marvellous of biological commonplaces—that the individual life of the great majority of plants and animals begins in the union of two minute elements—the sperm-cell and the egg-cell. These microscopic individualities unite to form a new individuality, a potential offspring, which will by-and-by develop into a creature like to, and yet different from its parents. If we mean by inheritance

to include all that the living creature is or has to start with in virtue of its genetic relation to its parents and ancestors, then it is plain that the physical basis of inheritance is in the fertilised ovum. The fertilised egg-cell *is* the inheritance, and at the same time the potential inheritor. What might be compared to an inheritance of property as apart from the organism itself is the store of food which may be inside the egg, or round about it.

To the general fact stated in the preceding paragraph, a few exceptions must be made—*e.g.* for bananas which have no longer any seeds, for potatoes which are multiplied by cutting, for the drone-bees and summer green-flies who have mothers but no fathers, and for simple unicellular organisms in which there is no sexual reproduction; but the exceptions are trivial compared with the vast majority of living creatures, in regard to which it is certain that each life begins in a fertilised egg-cell.

An organic inheritance means so much, even when we use the comfortable word potentiality, that, although we are quite sure that the germ-cells constitute the physical basis of inheritance, we may consider for a moment the difficulty which rises in the minds of many when they are told that the egg-cell is often microscopic, and the sperm-cell often only $\frac{1}{100000}$th of the ovum's size. Can there be room, so to speak, in these minute elements for the complexity of organisation supposed to be requisite? And the difficulty will be increased if the current opinion be accepted that only the nuclei within these minute germ-cells are the true bearers of the hereditary qualities. Darwin spoke of the pinhead-like brain of the ant as the most marvellous little piece of matter in the world, but must we not rank as a greater marvel the microscopic germ-cells which contained potentially all the inherited qualities of that ant?

From one microscopic egg of a sea-urchin cut into three, Delage reared three larvæ. In another case he reared an embryo from $\frac{1}{37}$th of an egg. Twin animals are often developed from one egg. Wilson obtained quadruplets by shaking apart the

four-cell stage in the development of the lancelet. Marchal describes a "legion of embryos" developing from a single ovum of a peculiar Hymenopterous insect *Encyrtus*. In development, indeed, a half may be as good as a whole.

In reference to the difficulty raised in some minds by the minuteness of the physical basis, it may be recalled that the students of physics, who make theories regarding the sizes of the atoms and molecules which they have invented, tell us that the image of an ocean liner filled with framework as intricate as that of the daintiest watches does not exaggerate the possibilities of molecular complexity in a spermatozoon, whose actual size is usually very much less than the smallest dot on the watch's face. Secondly, as we learn from embryology that one step conditions the next, and that one structure grows out of another, there is no need to think of the microscopic germ-cells as stocked with more than *initiatives*. Thirdly, we must remember that every development implies an interaction between the growing organism and a complex environment without which the inheritance would remain unexpressed, and that the full-grown organism includes much that was not inherited at all, but has been acquired as the result of nurture or external influence.

The fact is that size does not count for much in these matters, and the difficulty that some beginners feel in believing that the inheritance of the whale is packed into a pinhead-like egg is mainly due to ignorance of what may be called the fine complexity, or from another point of view the "coarse-grainedness," which must form part of our conception of every speck of matter. Nowhere more than in biology are we made to feel that "a little may go a long way."

It should be noted that the degree of *visible* complexity, even in the microscopic nucleus of a germ-cell, is often very considerable. Thus Eisen observed in the nucleus of a species of salamander twelve chromosomes, each of six parts, and in each part six granules—altogether 432 visible units.

§ 2. *Diverse Modes of Reproduction*

In the preceding paragraph we have given prominence to what is true of the great majority of living creatures,—that a new life begins as a fertilised egg-cell. It is necessary, however, to refer to the other ways in which a new organism may arise, for some of them help us to understand what the hereditary relation means. The following scheme will probably serve to recall the familiar facts :

Multiplication

- *In unicellular organisms.*
  - By division into two.
  - By budding, a modified form of division.
  - By sporulation, or division into many units.

  The reproduction may be wholly asexual: (1) in the sense that there is nothing corresponding to fertilisation or amphimixis; and (2) in the sense that there are no special germ-cells. But in many unicellular organisms there are elaborate processes of amphimixis, and in colonial forms, like *Volvox*, there is a definite beginning of egg-cells and sperm-cells. Among the parasitic Sporozoa or Gregarines in the wide sense there is also a close approximation to the mode of sexual reproduction seen in most multicellular organisms. No hard-and-fast line can be drawn.

- *In multicellular organisms.*
  - I. Without special germ-cells—*e.g.* by division of the body, by giving off buds (and as the result of artificial cutting).
  - II. With special germ-cells :

  (*a*) Eggs from one parent are fertilised by sperms from another parent—heterogamy, the commonest mode ;

  (*b*) Eggs from one parent are fertilised by sperms from the same (hermaphrodite) parent—autogamy, a very rare mode.

  (*c*) Eggs may develop without fertilisation—parthenogenesis.

  [A multicellular organism may also multiply by spore-cells—specialised germ-cells, yet hardly equivalent to eggs—which do not require fertilisation.] *

* If we lay emphasis on the presence or absence of special reproductive elements, the classification of the modes of multiplication would read as follows:

- I. Without special reproductive elements.
  - Division, budding, etc., in most unicellulars.
  - Division, budding, etc., in some multicellulars.
- II. With special reproductive elements.
  - More or less distinct specialisation of reproductive elements in some unicellulars.
  - Specialised ova and spermatozoa in most multicellulars.
  - Formation of spore-cells in some multicellulars.

If we lay emphasis on the occurrence or non-occurrence of amphimixis (= fertilisation) the classification of the modes of reproduction would read as follows :

- I. Without any form of amphimixis.
  - Without special reproductive-cells: (*a*) division, budding, etc., in many unicellulars ; and (*b*) division, budding, etc., in some multicellulars.
  - With special reproductive-cells: (*a*) formation of spores in some multicellulars ; (*b*) parthenogenetic ova.
- II. With some form of amphimixis.
  - Without specialised reproductive elements, amphimixis occurs in most unicellulars.
  - With specialised reproductive elements, amphimixis occurs in a few unicellulars and in most multicellulars.

The reasons for lingering over the modes of reproduction—which it is confessedly difficult to arrange in a perfectly clear scheme—are (1) that our general view of the hereditary relation must be one which is applicable to all cases and not merely to the most frequent, and (2) that some of the simplest cases shed light upon the more complex. It is also important that we should make clear that the common phrases, "asexual reproduction" and "sexual reproduction," are somewhat ambiguous, since attention has to be directed to two distinct points—(*a*) whether there are specialised reproductive elements, and (*b*) whether there is any form of amphimixis.

§ 3. *The Hereditary Relation in Unicellular Organisms*

At what is called "the limit of growth," when the cell has attained to as much volume as its surface can adequately supply with food and oxygen, and so on, a unicellular organism normally divides into two, obviating the difficulties which would ensue if volume increased out of proportion to surface. The halves separate and grow. Two more or less exact replicas of the original unit result. It has been demonstrated that the division is often preceded by that intricate and orderly process of nuclear division, known as karyokinesis, which results in an equal partition of the nuclear constituents between the two daughter-cells. As each of the halves is in the strictest sense half of the organisation of the parent unit, we are not surprised that each should in appropriate environment grow into an almost exact image of the original whole. In most cases we have no methods subtle enough to detect any difference. There is complete hereditary resemblance, and it would be puzzling if it were otherwise. Even when the unit divides into many units (as in spore-formation), there is no puzzle in the fact that each reproduces the likeness of the original whole, except the puzzle of growth—of

life, which is at present insoluble. Analogies may be found in methods of treating chemical molecules so that one gets at the end of the operation twice as many molecules as one had to start with; or in the multiplication of crystals by breaking them into fragments and placing them in solutions of the same substance; but, at the present time, these analogies are of no particular service, since we do not understand the nature of living matter. That a fragment of a unicellular's organisation may, in an appropriate environment, reproduce an apparently perfect replica of the original unit, is not in any way explained by pointing out that there may be reproduction of like by like in the case of crystals or chemical molecules.

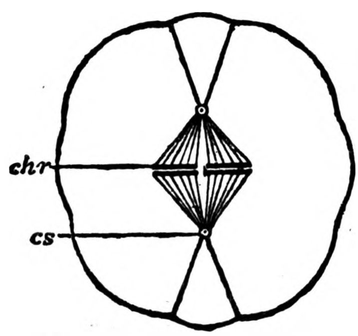

FIG. 2.—Diagram of cell division (after Boveri).
chr. chromosomes, forming an equatorial plate; *cs.* centrosome.

In slightly more complex cases there is a difference between the two units into which the unicellular organism divides. Thus, in the oblique division of the slipper animalcule (*Paramœcium*), the one half goes off with the "mouth," the other has none. In a short time, however, the mouthless half forms a "mouth," and each half grows into a replica of the original. But as the organisation of each half is essentially the same as, and directly continuous with the organisation of the original cell, the development of the halves into similar wholes presents no special difficulty. Similar organisation and similar surroundings yield similar results. That an injured infusorian should by re-growth repair its loss is an analogous phenomenon. Thus

we are led to see the force of Haeckel's definition of reproduction as discontinuous growth.

But in many unicellular elements, what is liberated to begin a new life is not a half of the original nor anything like it, but a minute unit often called a "spore." It also grows into a complete reproduction of the original. In such cases, we again try to make the matter more intelligible, by saying that each spore is a representative fragment of the organisation of the original unit, and will therefore, in appropriate surroundings, grow and differentiate as the original did. Exactly the same often occurs when the unicellular organism is artificially divided into several parts; and the results of these microscopic vivisection experiments, to which no one can on any grounds object, show that, if the excised fragment is to survive and develop, it must have a portion of the nuclear substance as well as of the general cell-substance. Without the nuclear constituent it may live for a time, as in *Stentor*, moving and responding to stimuli, but it cannot assimilate. Therefore, if we are asked what we mean by "organisation," we may say, at this stage, a certain protoplasmic architecture which implies essential relations between nucleoplasm and cytoplasm. The protoplasmic unit is like a firm with many partners of different kinds, each kind having many representatives; and the retention of vitality, the possibility of regeneration on the part of the fragments, has this for its essential condition, that the integrity of the firm—in which lies its secret—is maintained by each fragment having at least one representative of the different kinds of partners.

The reader who is not familiar with the subject should linger over the fact that a fragment or a minute spore, separated from a unicellular organism, may grow into (literally, *reproduce*) a unit, which to our senses is exactly like the original. This is (within the limits of our senses) *complete hereditary resemblance*, and we interpret it as due to the fact that the fragment or spore has to start with the essential organisation of the original. This

is, without complications, the fundamental fact in regard to inheritance.

It should also be borne in mind that many of the unicellular organisms (Protozoa, at the base of the animal series; Protophyta, at the base of the plant series) are highly differentiated—*i.e.* with great complexity of structure even within the narrow limits of size (where a diameter of $\frac{1}{100}$th of an inch is considered large)—and that many have very definite and interesting modes

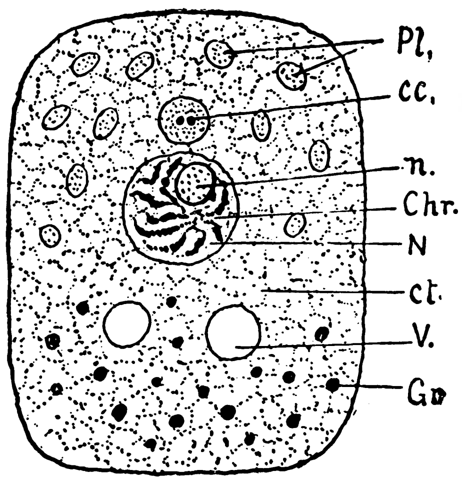

FIG. 3.—Diagram of cell structure. (After Wilson.)

Pl. Plastids in cytoplasm or cell-substance; *cc.* centrosome; *n.* nucleolus; *Chr.* chromosomes; *N.* nucleus; *ct.* general cytoplasm; *V.* vacuole; *Gr.* granules.

of behaviour, such as swimming in a spiral, seeking light or avoiding it, approaching certain substances and retreating from others, trying one kind of behaviour after another,—functional peculiarities—some of which cannot be described without using psychical terms—which are also included in the inheritance.

The case of a fragment of crystal growing into a complete crystal is interesting enough, but that a fragment or spore of apparent simplicity should reproduce the obvious complexity of the unit from which it was separated is relatively more marvellous.

A note is needed in regard to the misunderstanding which has led many to cite cases of inheritance in unicellulars as relevant to the discussion on the transmission of "acquired characters." Although we can no longer say that unicellular organisms are without sexual reproduction, since many exhibit the liberation of special reproductive units and the occurrence of amphimixis, we may still say that, apart from transitional forms (like *Volvox*, which form colonies or "bodies" of one thousand to ten thousand cells), there is among the unicellulars only the beginning of the important distinction between somatic or bodily and germinal or reproductive material which distinguishes multicellular organisms. This makes a notable difference.

§ 4. *The Hereditary Relation in the Asexual Multiplication of Multicellular Organisms*

In many of the simpler, but multicellular, plants and animals, a portion of the parent is separated off to form the beginning of a new life. The freshwater sponge multiplies in part by minute gemmules, which float away from the corpse of the parent and develop into new sponges; many polypes produce buds which may be set adrift, as in the freshwater Hydra, or may remain attached and help to form the great colonies that we see in zoophytes and Anthozoa; not a few worms also multiply by dividing or by budding, and the examples highest in the scale are found among the Tunicates, which are really vertebrate animals. Moreover, in some cases where asexual multiplication does not normally occur, it may still be a possibility, as is shown by the fact that cut-off portions may, in appropriate conditions, grow into entire individuals. Thus, two earthworms may occasionally be produced by cutting one; a sponge which does not normally liberate buds may be cut into pieces and bedded out successfully; the arms of the starfish, which

the fisherman tears asunder, may give rise to several new individuals. From nine excised fragments of a single Planarian worm, Voigt reared nine individuals (*see* Weismann, 1904, vol. ii. p. 25).

Similarly, in regard to plants, many of the simpler multicellular forms produce detachable buds, familiar in the case of the liverworts; and even in the flowering plants the same may occur, as in the bulbils of the tiger-lily. As in animals, great colonies may be formed, consisting of many individuals materially continuous, well seen in strawberries, whose creeping stems root here and there and give rise to independent plants. It is also a

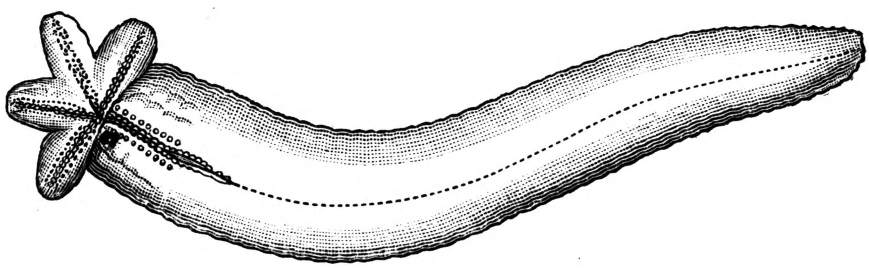

FIG. 4.—" Comet-form " of Starfish, showing how one arm regenerates the other four. (After Haeckel.)

familiar fact that cut-off portions of a plant may readily give rise to entire individuals; a little piece of moss, a Begonia leaf, a corner of a potato tuber—and hundreds of instances might be given—will suffice to start a new plant. In many ways the whole vegetable kingdom seems comparable to the sedentary sections of the class Cœlentera among animals (zoophytes, sea-anemones, corals, etc.), *e.g.* in the various forms of alternation of generations which occur, and in the readiness with which representative fragments will regrow the whole. This capacity of regenerating the whole from a small piece is the more striking when there is considerable differentiation of tissues and organs, as there is in flowering plants and the higher animals. The

fact being that the leaf of a plant, or a quarter of a zoophyte, or an eighth of a sea-anemone, may grow into an entire organism with reproductive cells, we must infer that the characteristic heritable material, usually segregated in the reproductive cells, is present in the cells of the body in these organisms.

The feature common to the ordinary forms of asexual multiplication is, that the reproduction is independent of eggs or sperms, or of any process comparable to fertilisation. What starts the new life, and forms in this case the material basis of

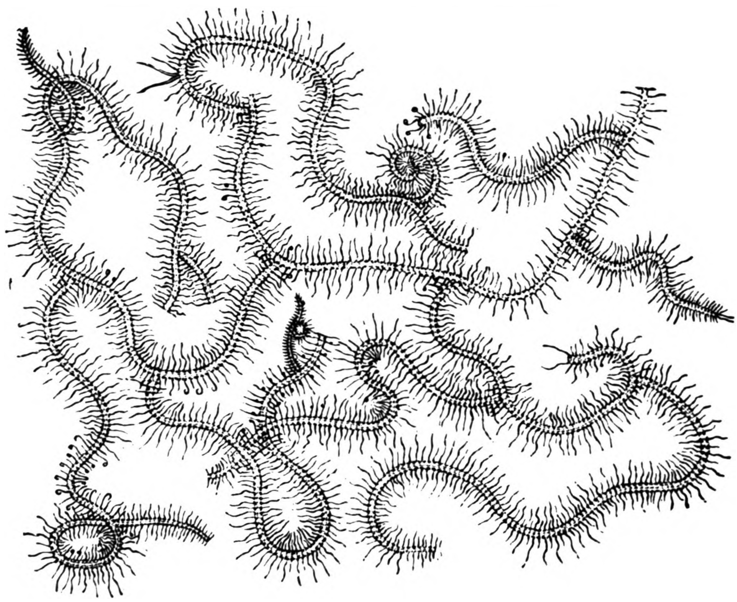

Fig. 5.—Asexual reproduction. A sea-worm (*Syllis ramosa*), in which budding has produced a branched temporary colony. (After McIntosh.)

inheritance, is a liberated portion of the parent. The heredity-relation is one of obvious material continuity.

As regards inheritance, the feature characteristic of asexual multiplication is that the resemblance between parent and offspring tends to be complete. As Sedgwick (1899) expresses it: "The offspring do not merely present resemblances to the parent—they are identical with it; and this fact does not appear to be astonishing when we consider the real nature of the process. Asexual reproduction consists in the separation of a portion of

the parent, which, like the parent, is endowed with the power of growth. In virtue of this property it will assume, if it does not already possess it, and if the conditions are approximately similar, the exact form of the parent. It is a portion of the parent; it is endowed with the same property of growth; the wonder would be if it assumed any other form than that of the parent."

In asexual reproduction the resemblance of the offspring to the parent tends to be very complete, and the reason for like producing like is no puzzle, when the separated off-portion is a representative sample of the whole organism.

§ 5. *Nature and Origin of the Germ-cells*

Re-statement of the Central Problem of Heredity.—The central problem of *inheritance* is to measure the resemblances and differences in the hereditary characters of successive generations, and to arrive, if possible, at formulæ which will sum up the facts, such as Galton's Law of Ancestral Inheritance and Mendel's Law. The central problem of *heredity* is to form some conception of what is essential in the relation of genetic continuity, which binds generation to generation. Weismann's theory of the continuity of the germ-plasm is, in the first instance, a theory of *heredity*, and as important as Galton's law of *inheritance*.

We know that almost every multicellular plant or animal has the beginning of its individual life in the union of two germ-cells (ovum and spermatozoon), and what must be found if the problem of heredity is to be illumined at all is some reason why the germ-cells should have this power of developing, and of developing into organisms which are on the whole like the parents. In what respects are the germ-cells peculiar, and

different from the ordinary cells of the body? Let us, then, concentrate our attention for a little on the nature and origin of the germ-cells.

It is inexpedient to lay on the shoulders of the student of heredity the burden of problems which are not in any special sense his business. It is no doubt interesting to ask how an organisation, supposed to be very complex, may be imagined to find physical basis in a microscopic germ-cell, but the same sort of question may be raised in regard to a ganglion-cell. It is not distinctively a problem of heredity. It is interesting to inquire into the orderly and correlated succession of processes by which the fertilised egg-cell gives rise to an embryo, but this is the unsolved problem of physiological embryology. It raises questions distinct from those of heredity and inheritance, and apparently much less soluble.

We shall return in the historical chapter to the various theories of heredity which have been suggested; in the meantime, we require to refer to them only in outline.

The Typical Ovum.—The germ-cell produced by the maternal parent is usually a relatively large sphere of living matter (cytoplasm), and various not-living included substances, such as nutritive yolk, pigment, oil-globules, and so forth. In the cytoplasm there lies a central kernel surrounded by a delicate membrane, the nucleus—a microcosm in itself. It contains a network or coil or some arrangement of delicate (linin) threads, carrying minute masses of a readily stainable material, the chromatin. Under high magnification the chromatin is seen to be built up of small corpuscles, sometimes like beads on a string, the microsomes. In certain phases of activity the chromatin forms a definite number of separate masses. They are then called chromosomes or idants, and the same number is usually present in all the cells of the body of any particular species. In the nuclear sap which fills the nucleus there is often a rounded body or vesicle—the nucleolus; or there may be

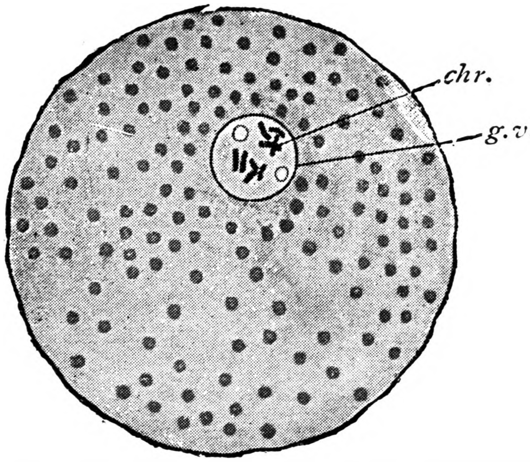

FIG. 6*a*.—Diagram of ovum, showing diffuse yolk-granules. *g.v.* germinal vesicle or nucleus; *chr.* chromosomes.

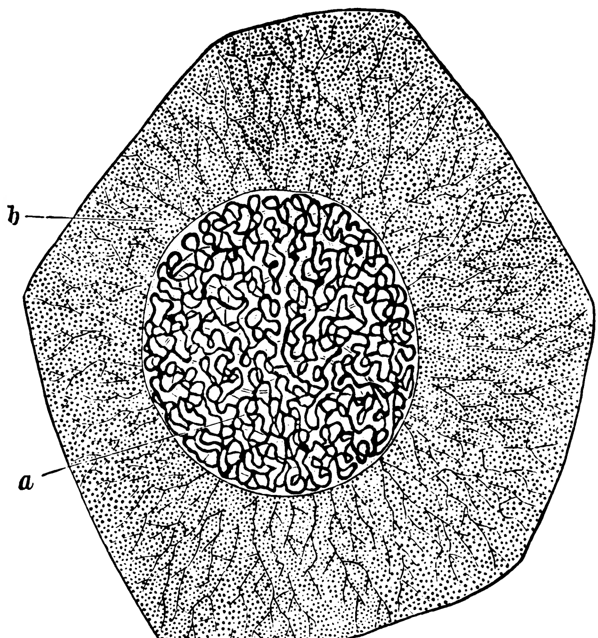

FIG. 6*b*.—Diagram of body-cell, showing the nucleus with coil of chromatin filaments and the surrounding cytoplasm. (After Carnoy.)

[*Facing p.* 38.

several nucleoli. As they are very variable and often transient, the nucleoli are not regarded as very important. Often they seem to be aggregations of reserve material or of waste-products.

The Typical Spermatozoon.—The germ-cell produced by the

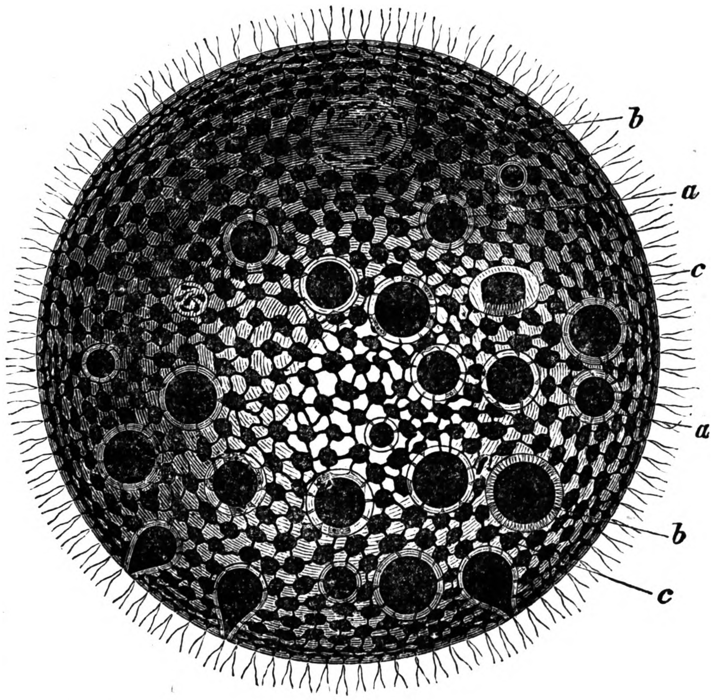

FIG. 7.—*Volvox globator*, an Infusorian forming a colony of cells, showing the ordinary cells (*c*) that make up the colony or incipient "body"; *a* and *b*, the special reproductive cells, both male and female—the beginning of the distinction between germ-cells and somatic cells.

male parent, the spermatozoon, is very different from the ovum in appearance and structure, and is also very much smaller. When the egg is swollen with yolk, which does not count as living material, the spermatozoon may be less than a millionth of its volume. Most of the cytoplasm of the spermatozoon forms a locomotor flagellum or tail, often of intricate structure, which drives the "head" or nucleus before it, always working against

a current if there is one. It is obviously a specialised adaptation which helps the spermatozoon to find the ovum, and it may be absent in cases where no journey or search is required. The so-called head of the spermatozoon contains the stainable material or chromatin, and in many cases it has been shown that the ripe spermatozoon has the same number of chromosomes as the ripe ovum. At the junction of the "head" and the "tail" there is a short "middle piece" or "neck," in which there is often seen a minute "centrosome."

There is in animals in most cases a great superficial contrast between the two kinds of germ-cells when fully mature. The typical ovum is relatively large, often laden with yolk, usually passive, and surrounded by some sort of membrane. The typical spermatozoon is relatively very minute, with no reserve material, and adapted to active locomotion. It is significant, however, that both contain the same number of chromosomes.

Old Attempts to interpret the Uniqueness of the Germ-cells.—In the preformationist theories, which held sway in the seventeenth and eighteenth centuries—theories which asserted the pre-existence of the organism and all its parts, in miniature, within the germ—there was a kernel of truth well concealed within a thick husk of error. For we may still say, as the preformationists did, that the future organism is implicit in the germ, and that the germ contains not only the rudiment of the adult organism, but the potentiality of successive generations as well. But what baffled the earlier investigators was the question, How the germ-cell comes to have this ready-made organisation, this marvellous potentiality. Discovering no natural way of accounting for this, the majority fell back upon a hypothesis of hyperphysical agencies—that is to say, they abandoned the scientific method, and drew cheques upon that bank where credit is unlimited as long as credulity endures.

An attempt to solve the difficulty which confronted the preformationists—the difficulty of accounting for the complex organisation presumed to exist in the germ-cell—is expressed in a theory which seems to have occurred at intervals in the long period between Democritus and Darwin, *the theory of pangenesis.* On this theory the cells of the body are supposed to give off characteristic and representative gemmules; these are supposed to find their way to the reproductive elements, which thus come to contain, as it were, concentrated samples of the different components of the body, and are therefore able to develop into

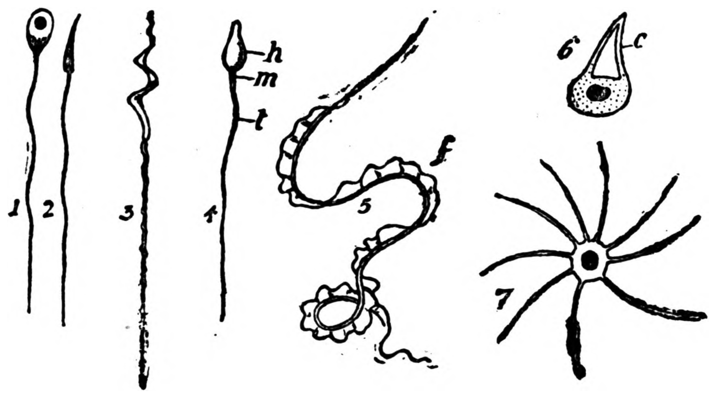

FIG. 8.—Forms of spermatozoa, enormously magnified, not drawn to scale.

1 and 2, Immature and mature spermatozoa of snail; 3, of bird; 4, of man—*h.* head, *m*, middle portion, *t*, tail; 5, of salamander, with vibratile fringe (*f*); 6. of Ascaris, slightly amœboid, with cap (*c*); 7, of crayfish.

an offspring like the parent. The theory is avowedly unverifiable in direct sense-experience, but the same may be said of many other hypotheses, and is not in itself a serious objection. It is more to the point to notice that it involves many hypotheses, some of them difficult to accept even provisionally. Galton long ago tried, by experiments on the transfusion of blood, to test one of these hypotheses, and found no confirmation. But it is still more to the point to notice that there is another theory of

heredity which is, on the whole, simpler—which seems, on the whole, to fit the facts better, for instance the fact that our experience does not warrant the conclusion that the modifications or acquired characters of the body of the parent affect in any specific and representative way the inheritance of the offspring.

The Idea of Germinal Continuity.—As is well known, the view which many, if not most, biologists now take of the uniqueness of the germ-cells is rather different from that of pangenesis. It is expressed in the phrase "germinal continuity," and has been independently suggested by several biologists, though Weismann has the credit of working it out into a theory. Let us state its purport. There is a sense, as Galton says, in which the child is as old as the parent, for when the parent's body is developing from the fertilised ovum, a residue of unaltered germinal material is kept apart to form the future reproductive cells, one of which may become the starting-point of a child. In many cases, scattered through the animal kingdom, from worms to fishes, the beginning of the lineage of germ-cells is *demonstrable* in very early stages before the differentiation of the body-cells has more than begun. In the development of the threadworm of the horse, according to Boveri, the very first cleavage divides the fertilised ovum into two cells, one of which is the ancestor of *all* the body-cells, and the other the ancestor of *all* the germ-cells. In other cases, particularly among plants, the segregation of germ-cells is not demonstrable until a relatively late stage. Weismann, generalising from cases where it seems to be visibly demonstrable, maintains that in all cases the germinal material which starts an offspring owes its virtue to being materially continuous with the germinal material from which the parent or parents arose. But it is not on a continuous lineage of recognisable germ-cells that Weismann insists, for this is often unrecognisable, but on the continuity of the germ-plasm—that is, of a specific substance of definite chemical and molecular structure which is the bearer

of the hereditary qualities. In development a part of the germ-plasm, "contained in the parent egg-cell, is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation." Thus the parent is rather the trustee of the germ-plasm than the producer of the child. In a new sense, the child is "a chip of the old block." As Sir Michael Foster put it, "The animal body is in reality a vehicle for ova; and after the life of the parent has become potentially

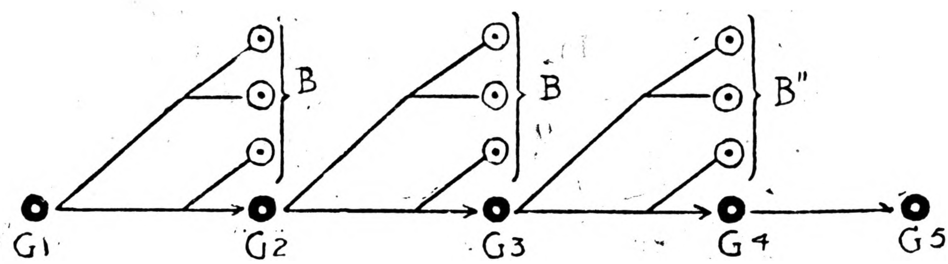

FIG. 9.—Diagram illustrating idea of germinal continuity. (After E. B. Wilson.)

G[1], fertilised ovum dividing into lineage of body-cells (B) and lineage of germ-cells—the base line; B′, B″, the bodies of two successive generations; G[1], G[2], G[3], G[4], G[5], the chain of germ-cells.

renewed in the offspring, the body remains as a cast-off envelope whose future is but to die." To use another metaphor, the germ-plasm is the lighted torch handed on from one runner to another. "Et quasi cursores vitaï lampada tradunt."

Early segregation of the germ-cells is in many cases an *observable* fact—and doubtless the list of such cases will be added to; but the conception of a germ-plasm is hypothetical, just as the conception of a specific living stuff or protoplasm is hypothetical. In the complex microcosm of the cell we cannot point to any one stuff and say, "This is protoplasm"; it may well be

that vital activity depends upon several complex stuffs which, like the members of a carefully constituted firm, are characteristically powerful only in their inter-relations. In the same way, it must be clearly understood that we cannot demonstrate the germ-plasm, even if we may assume that it has its physical basis in the stainable nuclear bodies or chromosomes. The theory has to be judged, like all conceptual formulæ, by its adequacy in fitting facts.

Let us suppose that the fertilised ovum has certain qualities, *a*, *b*, *c* . . . *x*, *y*, *z*; it divides and re-divides, and a body is built up; the cells of this body exhibit division of labour and differentiation, losing their likeness to the ovum and to the first results of its cleavage. In some of the body-cells the qualities *a*, *b*, find predominant expression, in others the qualities *y*, *z*, and so on. But if, meanwhile, there be certain germ-cells which do not differentiate, which retain the qualities *a*, *b*, *c* . . . *x*, *y*, *z*, unaltered, which keep up, as one may say figuratively, "the protoplasmic tradition," these will be in a position by-and-bye to develop into an organism like that which bears them. Similar material to start with, similar conditions in which to develop—*therefore*, like tends to beget like.

May we think for a moment of a baker who has a very precious kind of leaven; he uses much of this in baking a large loaf; but he so arranges matters by a clever contrivance that part of the original leaven is always carried on unaltered, carefully preserved for the next baking. Nature is the baker, the loaf is a body, the leaven is the germ-plasm, and each baking is a generation.

§ 6. *Maturation of the Germ-cells*

We have seen that the germ-cells owe their capacity of development to the fact that they are the unspecialised descendants of the parental fertilised ovum—the custodians of the characteristic germ-plasm. In some cases the lineage of germ-cells is from the first distinct and apart from the lineage of body-forming cells, and we argue from these clear cases of germinal continuity to the more numerous and less obvious cases where the germ-cells are not recognisable as such until later stages in development.

There is no need for our present purpose to follow the generations of the germ-cells within the body, or to trace the stages of growth and differentiation between primitive germ-cells and the fully formed ripe ova and spermatozoa. It is necessary, however, to allude to the process of maturation, which has a direct bearing on the problems of heredity and inheritance.

Maturation.—1. It is an elementary fact of histology that the nucleus of each cell in the body of an organism contains a number of readily stainable bodies or chromosomes. In many cases it has been possible to count these, and it has been found that (with a few explicable exceptions) the number is *constant for each species.*

As Prof. E. B. Wilson says (1900, p. 67): "The remarkable fact has now been established with high probability that *every species of plant or animal has a fixed and characteristic number of chromosomes, which regularly recurs in the division of all of its cells, and in all forms arising by sexual reproduction the number is even.** Thus, in some of the sharks the number is 36; in certain Gasteropods it is 32; in the mouse, the salamander, the trout, the lily, 24; in the worm *Sagitta*, 18; in the ox, guinea-

* In a few insects the females have in their body-cells one chromosome in addition to the number possessed by the males.

pig, and in man the number is said to be 48, and the same number is found in some snails. In the grasshopper it is 12; in the hepatic *Pallavicinia* and in some of the nematodes, 8; and in *Ascaris*, another thread-worm, 4 or 2. In the crustacean *Artemia* it is 168. Under certain circumstances, it is true, the number of chromosomes may be less than the normal in a given species; but these variations are only apparent exceptions [p. 87, Wilson]. The even number of chromosomes is a most interesting fact, which, as will appear hereafter [p. 205, Wilson], is due to the derivation of one-half the number from each of the parents."

2. About 1883, Van Beneden made the important discovery that the nuclei of the ovum and of the spermatozoon which unite in fertilisation contain each one-half of the number of chromosomes characteristic of the body-cells. This has been confirmed in regard to so many plants and animals that it may now be regarded as a general fact. The student should refer to the partial list given by Wilson (1900, pp. 206-7), where it will be seen that if the somatic nuclei have 12, 16, 18, or 24 chromosomes, the germ-nuclei have 6, 8, 9, or 12 respectively. A striking case is found in the large thread-worm (*Ascaris megalocephala*) of the horse, which occurs in two varieties,—the one, var. *univalens*, with two chromosomes in its body-cells has one chromosome in its germ-nuclei; the other, var. *bivalens*, with four chromosomes in its body-cells, has two chromosomes in its germ-nuclei.

3. If each of the nuclei which unite in fertilisation has only half as many chromosomes as are characteristic of the species, it follows that a reduction of the number must take place in the history of the germ-cells, and this is the outstanding fact in the process of maturation. Alike in the history of the egg (oogenesis) and in the history of the sperm (spermatogenesis),

there is a parallel reduction in the number of chromosomes to one-half.

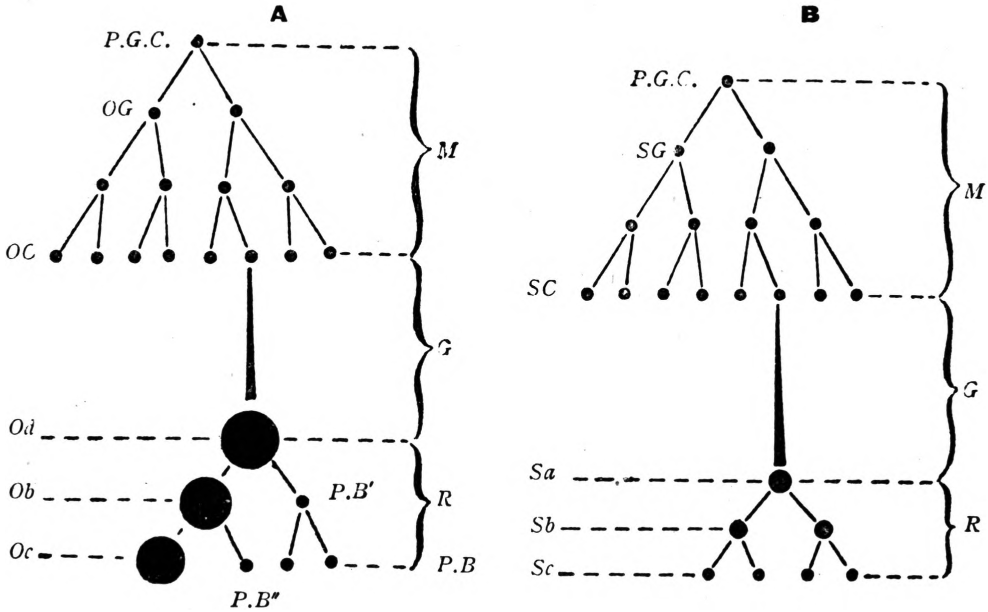

FIG. 10.—Parallelism of oogenesis (**A**) and spermatogenesis (after Boveri).

P.G.C. in both series (**A** and **B**), one of the primitive germ cells.
Following the oogenesis (**A**), there is first of all a period of multiplication (*M*), included within the first bracket.
The primitive germ-cell gives rise to oogonia (*OG*).
These oogonia give rise to oocytes (*OC*).
Then follows a period of growth (*G*), included within the second bracket.
Then follows the process of ripening or maturation (*R*), included within the third bracket.
Od, the immature ovum, with the normal number of chromosomes.
P.B', the first polar body, usually separated off by a meiotic or reducing division which lessens the number of chromosomes to one half the normal.
Ob, the ovum after giving off the first polar body, with half the normal number of chromosomes.
P.B", the second polar body, formed by an ordinary equation division.
Oc, the ripe ovum.
P.B', the first polar body has divided into two by an equation division.
Following the spermatogenesis (**B**), there are successive periods (or zones in the testis) of multiplication (*M*), growth (*G*), and reduction (*R*).
The primitive germ-cell gives rise to spermatogonia (*SG*).
These spermatogonia give rise to spermatocytes (*SC*).
Immature spermatocytes of the first order (*Sa*) have the normal number of chromosomes. In many cases by a reduction or meiotic division they give rise to spermatocytes of the second order (*Sb*), with half the normal number of chromosomes.
These give rise by an equation division to spermatozoa (*Sc*).

"The one fact of maturation that stands out with perfect clearness and certainty amid all the controversies surrounding it is *a reduction of the number of chromosomes in the ultimate germ-cells to one-half the number characteristic of the somatic cells.* It is equally clear that this reduction is a preparation of the germ-

cells for their subsequent union and a means by which the number of chromosomes is held constant in the species. With a few exceptions the first indication of the numerical reduction appears through the segmentation of the spireme-thread, or the resolution of the nuclear reticulum, into a number of masses *one-half that of the somatic chromosomes.* In nearly all higher animals this process first takes place two cell-generations before the formation of the definitive germ-cells, and the process of reduction is completed by two rapidly succeeding 'maturation-divisions,' giving rise to four cells, all of which become functional in the male, while in the female only one becomes the egg, and the other three—the polar bodies or their analogues—are cast aside. During these two divisions each of the original chromatin masses gives rise to four chromosomes, of which each of the four daughter-cells receives one; hence, each of the latter receives one-half the somatic number of chromosomes. In the higher plants, however, the two maturation-divisions are followed by a number of others, in which the reduced number of chromosomes persists, a process most strikingly shown in the pteridophytes, where a separate sexual generation (prothallium) thus arises, all the cells of which show the reduced number" (Wilson, 1900, p. 285).

The asexual spore-bearing fern-plant has in its cells twice as many chromosomes ($2n$) as the sexual prothallus has (n). The spores produced by the fern-plant have n chromosomes; they develop into a prothallus with n chromosomes; the prothallus produces sex-cells with n chromosomes; these undergo no reduction and by their union they restore the number $2n$, which characterises the resulting embryo and the subsequent fern-plant.

As Boveri has said: "Thus at some stage or other in the generation-series of the germ-cell there occurs a reduction of the number of chromosomes originally present to one-half, and this *numerical* reduction is therefore to be regarded, not as a mere theoretical postulate, but as a fact" (*Zellen-Studien*, iii. 1890, p. 62).

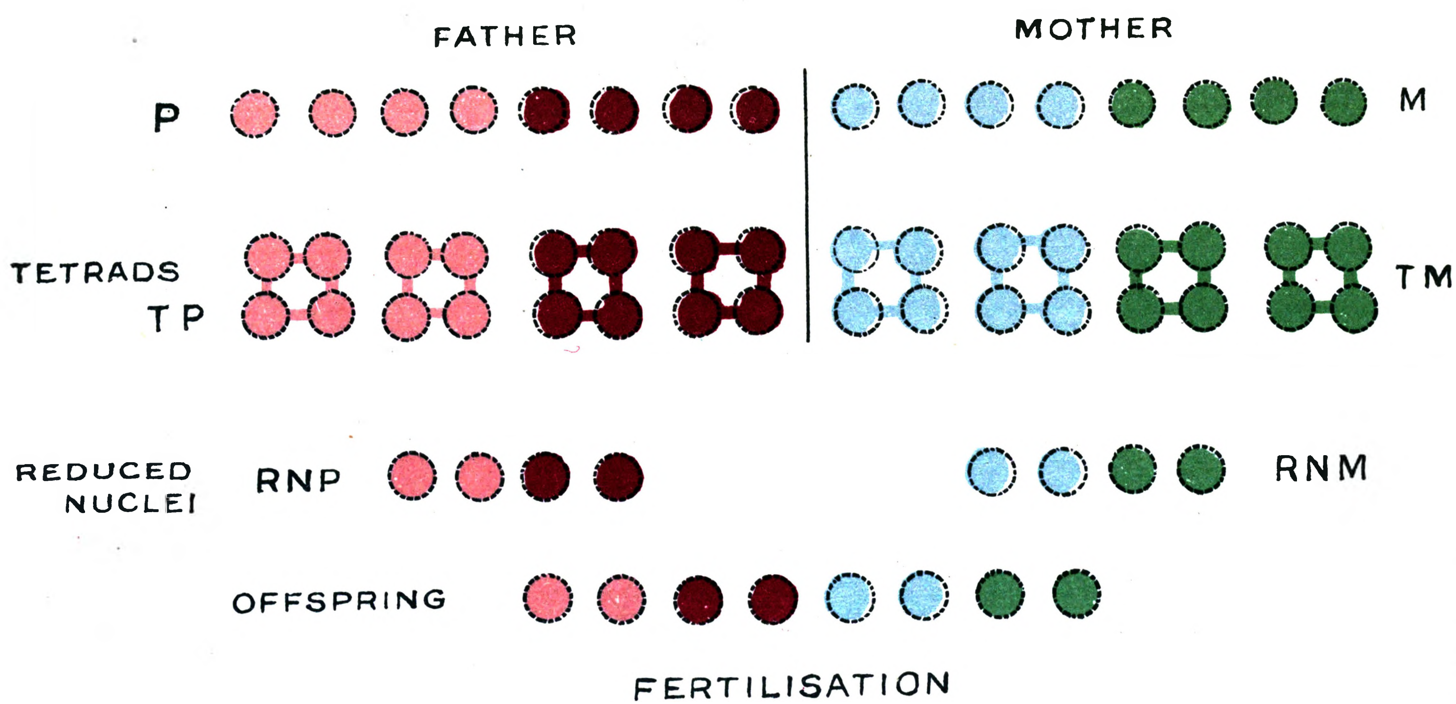

Fig. 11.—Diagram to illustrate reduction of chromosomes and amphimixis. (After H. E. Ziegler.)

P, paternal chromosomes, supposed to be eight in number and of two sets, the light red from the paternal grandfather, the deep red from the paternal grandmother; M, Maternal chromosomes supposed to be eight in number and of two sets: the blue from the maternal grandfather, the green from the maternal grandmother; TP and TM, Tetrads formed in maturation; RNP, the four chromosomes of the reduced nucleus of the ripe spermatozoon; RNM, the four chromosomes of the reduced nucleus of the ripe ovum. In the offspring there are eight chromosomes, four paternal, four maternal, and of four different sets—contributions from the four grandparents. In this case four *other* combinations are possible so that there might be five different kinds of offspring.

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§ 7. *Amphimixis and the Dual Nature of Inheritance in Sexual Reproduction*

Apart from exceptional cases, the inheritance of a multicellular animal or plant is dual—part of it comes from the mother and part of it from the father; in other words, the material basis of inheritance is a fertilised egg-cell. The new individuality has its origin in the fusion of two potential individuals, for as such the ovum and spermatozoon must be regarded. The exceptions referred to are cases of asexual multiplication by buds or otherwise, as in the freshwater Hydra; cases of parthenogenesis, as in the case of the unfertilised eggs which develop

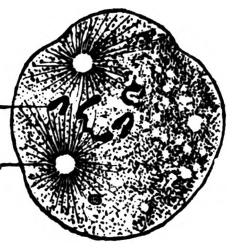


FIG. 12.—Fertilised ovum of *Ascaris*. (After Boveri.)

chr. chromosomes, two from ovum-nucleus and two from sperm-nucleus; *cs*. centrosome, from which "archoplasmic" threads radiate, partly to the chromosomes.

into green flies (Aphides) in the summer; and cases like liver-flukes, where an animal is both mother and father to its offspring. Apart from these exceptions the inheritance does at the start consist of maternal and paternal contributions in intimate and orderly union.

When a spermatozoon, outstripping its fellows (for there are usually very large numbers), reaches an ovum and bores its way into it, the cytoplasmic flagellum is left behind, having performed its function, and the sperm-nucleus and the ovum-nucleus move towards one another. By a rapid change in the periphery of the ovum, the enveloping membrane becomes firmer, and the ovum becomes non-receptive to other spermatozoa. When

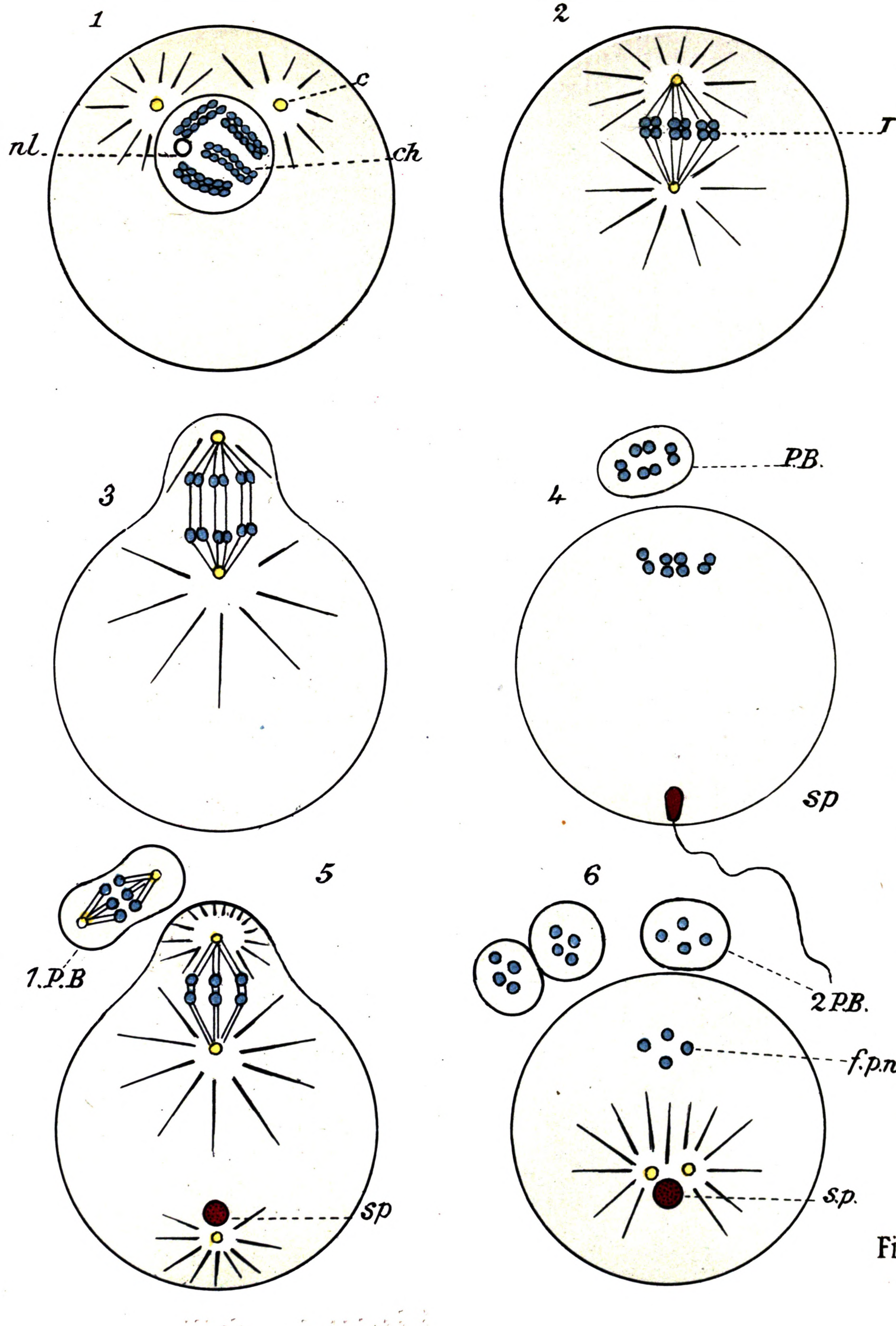
several effect entrance at once, abnormalities usually result. In the mature ovum there is no centrosome ; if it was originally present, it disappears. The spermatozoon, however, introduces, along with its nucleus, its centrosome, and this divides into two. The two centrosomes appear to take an active part in the approximation and intimate apposition of the maternal and paternal chromosomes, and in their subsequent partition between the first two daughter-cells.

Prof. E. B. Wilson states the general opinion of experts somewhat as follows. As the ovum is much the larger, it is believed to furnish the initial capital—including, it may be, a legacy of food-yolk—for the early development of the embryo. From both parents alike comes the inherited organisation which has its seat (according to most biologists) in the readily stainable (chromatin) rods of the nuclei. From the father comes a little body (the centrosome) which organises the machinery of division by which the egg splits up, and distributes the dual inheritance equally between the daughter-cells.

Let us now proceed to expound four important theorems.

1. **In Ordinary Sexual Reproduction the Inheritance is very precisely Dual or Biparental.**—Recent discoveries have shown that the paternal and maternal contributions which come together in fertilisation are, for several divisions at least, exactly divided among the daughter-cells, thus confirming a prophecy which Huxley made in 1878 : "It is conceivable, and indeed probable, that every part of the adult contains molecules derived both from the male and from the female parent ; and that, regarded as a mass of molecules, the entire organism may be compared to a web of which the warp is derived from the female and the woof from the male." "What has since been gained," Prof. Wilson says, "is the knowledge that this web is to be sought in the chromatic substance of the nuclei, and that the centrosome is the weaver at the loom."

After the paternal and maternal chromosomes have united,



Fig

FIG. 13.—Diagram of maturation and fertilisation and first stages of cleavage. (From Prof. H. E. Ziegler, with his kind permission.) The colours have been added.

1.—The immature ovum, with four double chromosomes, longitudinally cleft; *c*, centrosome; *ch*, chromosomes; *nl*, nucleolus.

2.—First maturation division; the nuclear spindle has at its equator four groups of tetrads, three of which are visible.

3 and 4.—Formation of the first polar body (P.B.). In fig. 4 a spermatozoon (*sp*) is entering. The paternal chromatin is shown throughout in red, the maternal in blue, the centrosome which is brought in by the spermatozoon is shown in yellow. The ovum-centrosome disappears.

5.—The formation of the second polar body and the division of the first (1 *P.B.*). The head of the spermatozoon has formed the male pronucleus (*sp*). The centrosome introduced by the spermatozoon is surrounded by a clear area and rays.

6.—The second polar body (2 *P.B.*) has been set adrift. The first has divided into two. The three polar bodies and the now mature ovum have in their nuclei half the normal number of chromosomes. Thus four are seen in the female pronucleus (*f.pn*). The centrosome has divided into two.

7.—The male and female pronuclei (*sp* and *f.pn*) have become like one another, and are near together. The centrosomes (*c*) have become the centres of two large systems of rays.

8.—The two pronuclei are in contact and are coalescing.

9.—The nuclei have lost their membrane, and the first segmentation-spindle or cleavage-spindle has been formed, a centrosome lying at each pole. The spindle has the normal number of chromosomes, but each has divided, so that eight pairs are present.

10.—The egg-cell is dividing. The chromosomes are separated into two groups, each group with eight chromosomes. The centrosome at each pole has divided into two.

11.—The division or cleavage is complete. The rays have disappeared. The chromosomes are represented by minute vesicles or karyomeres.

12.—The new nuclei have been constituted by union of the vesicles. The centrosomes lie closely apposed, but will occupy the poles of the spindle at the next division.

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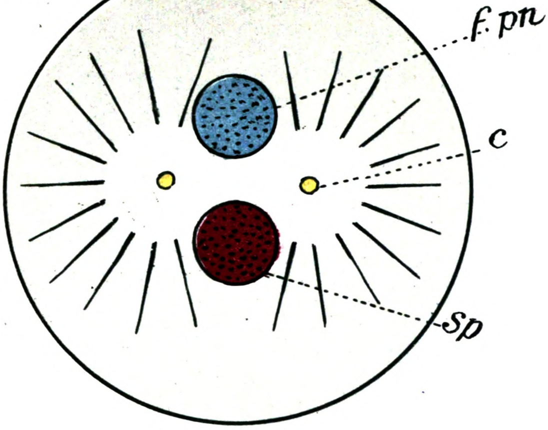

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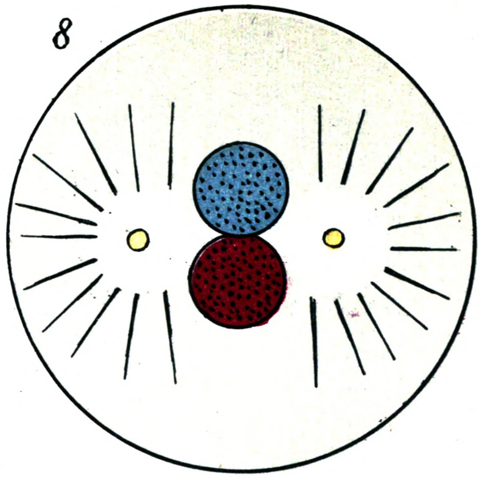

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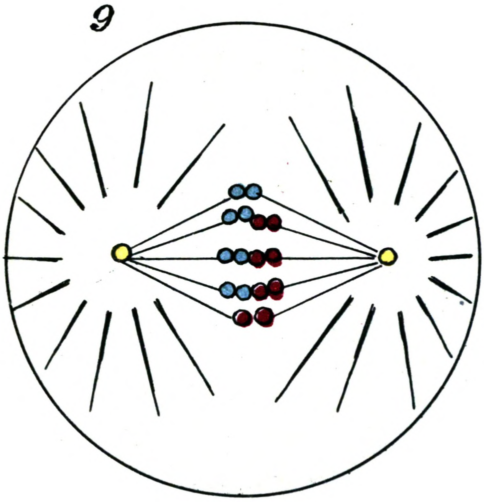

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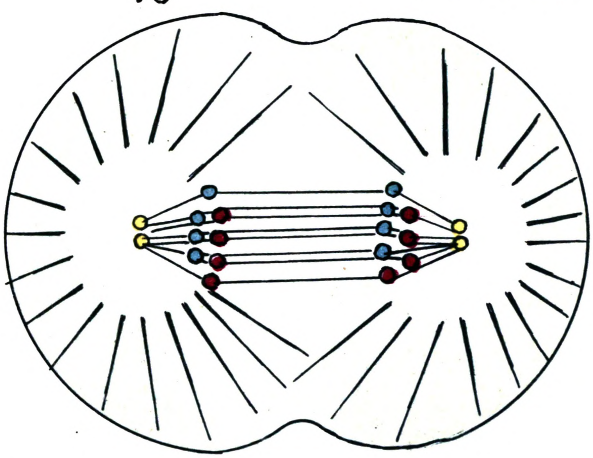

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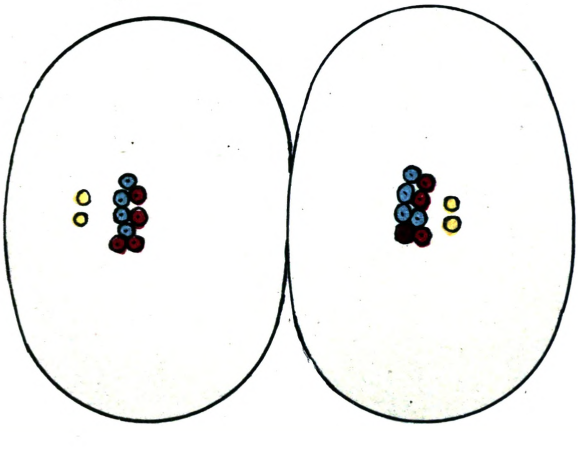

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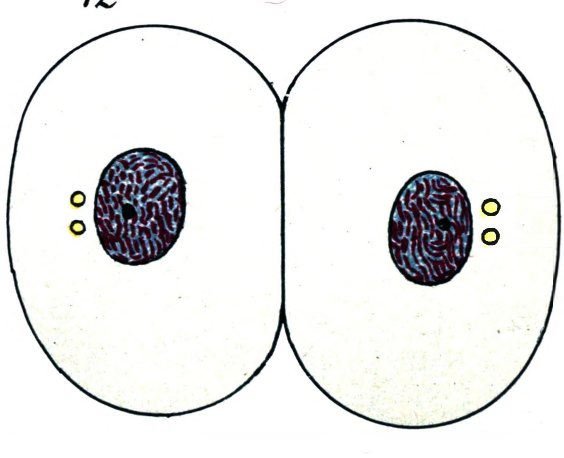

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but never fused, to form one nucleus—the segmentation-nucleus—the cleavage or segmentation of the fertilised ovum begins.

There is a centrosome, derived from the sperm-centrosome, at each pole of the nucleus, and a system of fine rays radiates from each, some of these rays entering into close association with the chromosomes.

Each chromosome is halved *longitudinally*, as a piece of stick might be split up the middle, and after a very complex routine the halves of each split chromosome migrate, either actively or passively, to opposite poles. Thus, near each centrosome there comes to be a group of chromosomes, half of each group being of paternal origin and half of maternal origin. Each group in an orderly fashion rounds itself off into a unified nucleus, the body of the cell (the cytoplasm) constricts across the equatorial plane, and two cells are formed.

The gist and import of the whole process is the precisely equal partition of the maternal and paternal contributions, so that each of the daughter-cells has a nucleus half maternal and half paternal. For many successive divisions (*e.g.* in *Cyclops*) the duality has been demonstrated,* so that we may fairly say that the maternal and paternal contributions form the warp and woof of the growing organism.

2. **Inheritance, though Dual, is strictly Multiple.**—Although the whole inheritance which constitutes an offspring usually comes from two parents, and may therefore be called dual, it is obvious that the heritable material of each parent was also dual, being derived from the grandparents, and so on backwards; so that inheritance is strictly not merely dual, but in an even deeper sense multiple. Amphimixis or fertilisation implies the subtle mingling of two minute organisations so that they become physiologically one, but each of them was already

* According to Haecker's careful observations on the water-flea *Cyclops*, the paternal and maternal contributions, *i.e.* chromosomes, are traceable as distinct individualised items throughout the whole of development.

the complex product of ancestral lineage. We shall return to the subject when we come to consider Galton's Law of Ancestral Inheritance.

Though a comparison with the inheritance of property is apt to mislead, it may be of use to think for a moment of a youth inheriting an estate, of which one might accurately say that it had belonged in half to his father and in half to his mother. Yet a genealogist with a full knowledge of the family might be able to go further back, and might show, with even greater accuracy, how this corner was due to a grandmother and that to a great-grandfather.

This conception is so fundamentally important that I cannot refrain from quoting an illustration from Mr. Galton's *Natural Inheritance,* which puts the matter very clearly. "Many of the modern buildings in Italy are historically known to have been built out of the pillaged structures of older days. Here we may observe a column or a lintel serving the same purpose for a second time, and perhaps bearing an inscription that testifies to its origin; while as to the other stones, though the mason may have chipped them here and there and altered their shape a little, few if any came direct from the quarry. . . . . This simile gives a rude though true idea of the exact meaning of Particulate Inheritance—namely, that each piece of the new structure is derived from a corresponding piece of some older one, as a lintel was derived from a lintel, a column from a column, a piece of wall from a piece of wall. . . . We appear to be severally built up out of a host of minute particles of whose nature we know nothing, any one of which may be derived from any one progenitor, but which are usually transmitted in aggregates, considerable groups being derived from the same progenitor. It would seem that while the embryo is developing itself, the particles more or less qualified for each post wait, as it were, in competition to obtain it. Also that the particle that succeeds must owe its success partly to accident of position and partly to

being better qualified than any equally well-placed competitor to gain a lodgment. Thus the step-by-step development of the embryo cannot fail to be influenced by an incalculable number of small and mostly unknown circumstances." (*Natural Inheritance*, p. 9.)

3. **Duality of Inheritance may be real, though it is not expressed.**—It must be carefully observed that the demonstration of the dual nature of inheritance afforded by the facts of amphimixis does not necessarily imply that the dual nature of the inheritance will be patent in the full-grown offspring. The offspring is often like both its parents, often particularly like one, often not very like either. The parent of children, the breeder of animals, or the cultivator of plants, has often occasion to remark in the offspring what looks like an entire absence of the characteristics of one of the parents. The foal may seem to take entirely after the sire, as if the maternal inheritance counted for nothing. It is likely that this so-called "exclusive" or "unilateral" inheritance is often more apparent than real, our observation being arrested and preoccupied by a few outstanding features. The certain fact that the resemblance, apparently absent, often reappears in the next generation, shows that the incompleteness was not in these cases in the inheritance, but simply in its expression. We shall return to this subject in connection with the different modes of inheritance.

4. **Each Germ-cell has a Complete Equipment of Hereditary Qualities.**—It is usually assumed that each of the two sex-cells which unite in fertilisation has in it the potentiality of an organism with a full equipment of the essential characters of the species; but since the spermatozoon always dies unless it enters the ovum, it is difficult to give experimental proof of the assumption. Some recent daring experiments, which demand confirmation, are very suggestive in this connection.

Prof. Yves Delage (1898) divided the minute egg of the sea-urchin under the microscope into two parts, one containing the

nucleus and its companion-body the centrosome, the other being necessarily simply half of the living matter of the egg without any nucleus. Beside them he placed an intact ovum, and then let the spermatozoa in. All the three objects showed equal "sexual attraction" in respect to the spermatozoa; all three were fertilised; all three segmented, the intact ovum most rapidly, the nucleated fragment more slowly, the non-nucleated fragment more slowly still. In one case the development proceeded for three days; the intact ovum had become a typical gastrula (two-layered embryo), the nucleated fragment a smaller gastrula, and the non-nucleated fragment also a gastrula but with a very much reduced cavity. All the cells of these embryos showed nuclei. Thus the experimenter was led to the conclusion that *fertilisation and some measure of development may occur in a fragment of ovum without nucleus or centrosome.* The nucleus of the spermatozoon must have been in this case sufficient in itself, though it will be noticed that in the experiment cited the fragment did not develop far. Delage makes the important suggestion that in fertilisation two things must be distinguished: (*a*) the stimulus given to the ovum by some specially energetic substance brought in by the spermatozoon, perhaps in its centrosome; and (*b*) the mingling of heritable characteristics, Weismann's "amphimixis."

In subsequent experiments Prof. Delage (1899) reached even more extraordinary results. Non-nucleated fragments of the ovum of *Echinus* (sea-urchin), *Dentalium* (elephant's-tooth shell), and *Lanice conchilega* (a seashore worm), were effectively fertilised and gave rise to the characteristic larval forms—pluteus, veliger, and trochophore respectively. Three larvæ were reared from one ovum of a sea-urchin; a normal blastula embryo (a hollow ball of cells) was reared from $\frac{1}{37}$th of a sea-urchin ovum; a non-nucleated fragment of a sea-urchin ovum, after fertilisation by a spermatozoon with nine chromosomes (nuclear rods), gave rise to a larva whose cells had the

normal number of eighteen chromosomes: such are some of the extraordinary results reached by this clever experimenter. It seems, then, as if *fertilisation may, in many cases, be effective without there being any ovum-nucleus present,* as if the essential fact were the union of a sperm with a mass of egg-cytoplasm.

Delage's experiments cited above seem to prove that the nucleus and centrosome of the ovum are not essential to fertilisation. Professor Loeb (1899), of Chicago, has made experiments which seem to show that the spermatozoon may be dispensed with. In other words, he has been able to induce parthenogenetic development artificially in cases where it does not normally occur. He has been led to believe that the only reason why the eggs of many marine animals do not develop parthenogenetically is that something in the constitution of the sea-water prevents it. This something is the presence or absence of ions of sodium, calcium, potassium, and magnesium, the two former requiring to be reduced, the two latter to be increased. "The mixture of about 50 per cent. $\frac{10}{8}n$ $MgCl_2$ (magnesium chloride) with about 50 per cent. of sea-water was able to bring about the same effect as the entrance of a spermatozoon. The unfertilised eggs [of the sea-urchin *Arbacia*] were left in such a solution for about two hours. When brought back into normal sea-water they began to segment and form blastulæ, gastrulæ, and plutei, which were normal in every respect. The only difference was that fewer eggs developed, and that their development was slower than in the case of the normal development of fertilised eggs. With each experiment a series of control experiments was made to guard against the possible presence of spermatozoa in the sea-water. . . . From these experiments it follows that *the unfertilised egg of the sea-urchin contains all the essential elements for the production of a perfect pluteus.* The only reason that prevents the sea-urchin from developing parthenogenetically under normal conditions is the constitution of

the sea-water. The latter either lacks the presence of a sufficient amount of the ions that are necessary for the mechanics of cell division (Mg, K, HO, or others), or it contains too large a quantity of ions that are unfavourable to this process (Ca, Na, or others), or both. All the spermatozoon *needs* to carry into the egg for the process of fertilisation are ions to supplement the lack of the one or counteract the effects of the other class of ions in the sea-water, or both. The spermatozoon *may*, however, carry in addition a number of enzymes or other material. The ions and not the nucleins in the spermatozoon are essential to the process of fertilisation."

These remarkable experiments are confirmatory of the general assumption that spermatozoon and ovum are completely equipped potential organisms. Further confirmation may be found in cases of partial parthenogenesis—*e.g.* the development of drone-bees from unfertilised eggs; from the close similarity in the history of ovum and spermatozoon respectively; from the exactly equal way in which the paternal and maternal nuclear contributions are distributed to each cell, during the early stages of cleavage at least.

Or take the simple experiment of crossing a black guinea-pig with a typical albino. All the offspring are black, although only one of the parents—it does not matter which—has the quality of blackness. It is evident that the germ-cells of either parent are able to carry a complete equipment of blackness.

When we consider the ovum and spermatozoon as two fully equipped potential individualities which unite to form the beginning of a new individuality, we see more clearly how, on the one hand, there is a double likelihood of the essential specific characters being sustained, and how, on the other hand, there is every likelihood that the intermingling will lead indirectly, if not directly, to something new.

§ 8. *Inheritance in Cases of Parthenogenesis*

It would be interesting to know with precision what the facts of inheritance are in cases where development proceeds from an unfertilised ovum, particularly in those cases where the parthenogenesis continues uninterruptedly for many generations. On general grounds, from the absence of fertilisation, one would expect to find few new departures or progressive variations; but rather, on the other hand, hints of degeneracy. The observed facts are still very few.

Experiments which Prof. Weismann (1893, p. 344) made on a small crustacean (*Cypris reptans*) showed a very high degree of uniformity between parent and offspring, with occasional exceptions, which he regarded as exhibiting reversions to an ancestral form many generations removed.

Dr. Warren's (1899) measurements of successive parthenogenetic generations of *Daphnia magna* also gave evidence of slight variability (*i.e.* of incompleteness of hereditary resemblance). They seemed to favour the view that "inheritance in parthenogenetic generations resembles that from mid-grandparent to grandchildren."

§ 9. *Wherein the Physical Basis precisely consists*

The fertilised egg-cell divides into many cells; these arrange themselves in various ways; they grow and multiply; they exhibit division of labour and the structural side of this—which we call differentiation; they form tissues and organs; they become integrated into a body; they reproduce the likeness of the parental type with variations. Meanwhile, some of the cells remain apart from body-making or differentiation, and form the beginnings of the reproductive organs, whence their descendants—the mature germ-cells—are by-and-bye liberated to start another generation. That this next generation is also after the parental type is due to the continuous lineage of cells

containing unspecialised germinal material. In similar conditions similar material produces similar results.

But, if this has become clear, we have now to inquire into the precise nature of the physical basis which conserves the heritable qualities. Is it the germ-cell as a whole that is essential, or is the cytoplasm most important, or is it the nucleus only ?

Importance of the Chromosomes of the Germ-nuclei.—Many observations go to show that the nucleus of a cell plays an important part in nutritive and constructive processes, and it is certain that a cell artificially bereft of its nucleus will soon die if left to itself. The nuclear material (karyoplasm or nucleoplasm) is an essential part of the vital organisation. The view has gained ground that the chromatin bodies or chromosomes are the chief, if not the exclusive, vehicles of the hereditary qualities.

Let us consider some of the arguments in support of this view.

1. *Argument from cell-division.*—Roux, Hertwig, Kölliker, Strasburger, and many others, have emphasised the fact that, in the ordinary (mitotic) form of cell-division, the chromatin or readily stainable material of the nucleus is divided " with the most scrupulous equality " to form the basis of the nuclei of the daughter-cells, while the cytoplasm or general cell-substance " undergoes on the whole a mass-division—a most remarkable contrast." As Prof. Wilson says (1900, p. 351) : " This holds true with such wonderful constancy throughout the series of living forms, from the lowest to the highest, that it must have a deep significance. And while we are not yet in a position to grasp its full meaning, this contrast [between nuclear and cytoplasmic behaviour in division] points unmistakably to the conclusion that the most essential material handed on by the mother-cell to its progeny is the chromatin, and that this substance, therefore, has a special significance in inheritance."

2. *Argument from maturation.*—In the changes which lead up to the ripe egg and the fully-formed spermatozoon, there is, as we have seen, an elaborate preparation whereby the germ-nuclei which unite in fertilisation are rendered precisely equal as regards the number of their chromosomes. On the other hand, the cytoplasm of the relatively large, passive, often food-laden and ensheathed ripe ovum

is typically as different as possible from that of the very minute, actively mobile, usually short-lived spermatozoon. The constancy and frequent complexity of the reduction-processes which secure the equivalence of chromosomes suggest that these bodies are of paramount importance in inheritance.

3. *Argument from fertilisation.*—In typical cases of fertilisation in animals, and in many plants as well, a spermatozoon enters an ovum, sometimes a hundred thousand times larger than itself. As it enters it may leave behind it the locomotor "tail," which has

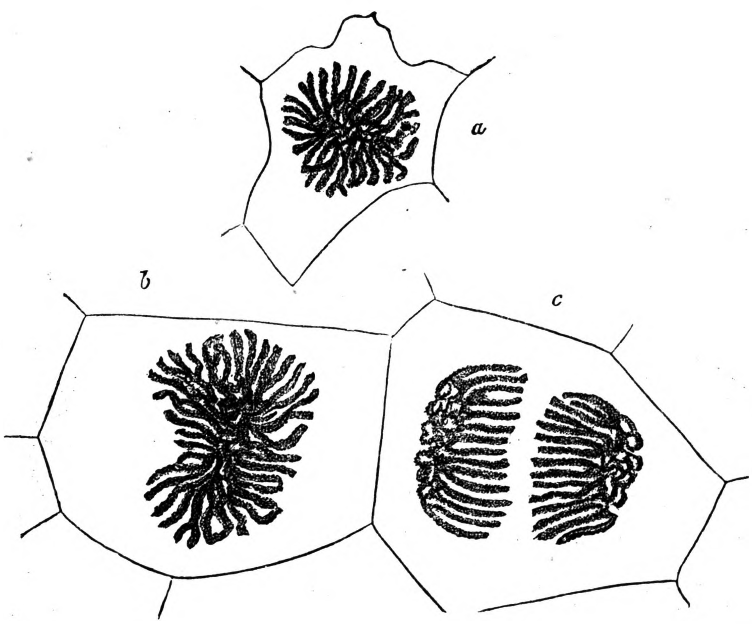


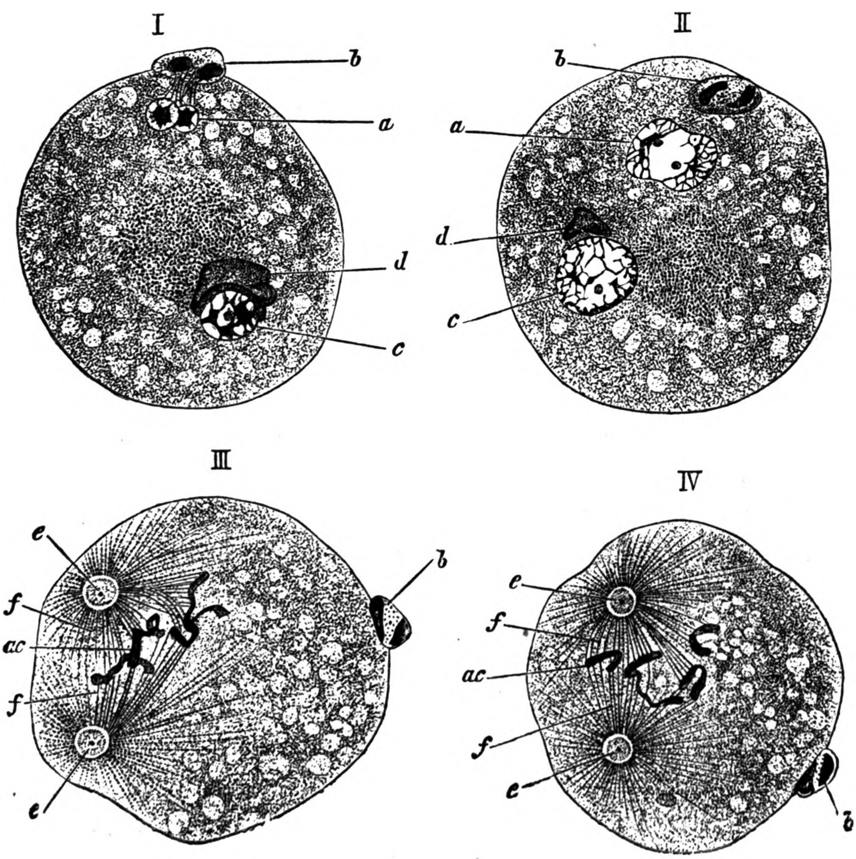
FIG. 14.—The chromatin elements of the nuclei in coil (*a*), double star (*b*), and almost divided stages (*c*). (After Pfitzner.)

discharged its function, thus further reducing its infinitely small stock of cytoplasmic material. The "head" of the spermatozoon, which is mostly nucleus, and the little "middle piece" which carries the centrosome, are apparently the important parts, and it is the ovum which furnishes the cytoplasmic basis of further operations. The very gist of fertilisation, *so far as we can see it*, is the intimate and orderly combination of the paternal and maternal chromosomes to form one nucleus—the segmentation-nucleus. Moreover, the maternal and paternal contributions are, as we have noted, distributed

with scrupulous equality, certainly to the first two cells of the embryo, and probably to all later-formed cells.

"The latter conclusion, which long remained a mere surmise, has been rendered nearly a certainty by the remarkable observations of Rückert, Zoja, and Haecker. We must, therefore, accept the high probability of the conclusion that the specific character of the cell is in the last analysis determined by that of the nucleus—that is, by the chromatin; and that in the equal distribution of paternal and maternal chromatin to all the cells of the offspring, we find the physiological explanation of the fact that every part of the latter may show the characteristics of either or both parents" (Wilson, 1900, p. 352).

4. *Argument from Boveri's ingenious experiment.*—Taking a hint from the experiments of the brothers Hertwig, who showed that non-nucleated fragments of unfertilised sea-urchin ova (broken by shaking) might be successfully fertilised and might segment, Boveri (1889, 1895) showed that such fertilised fragments developed



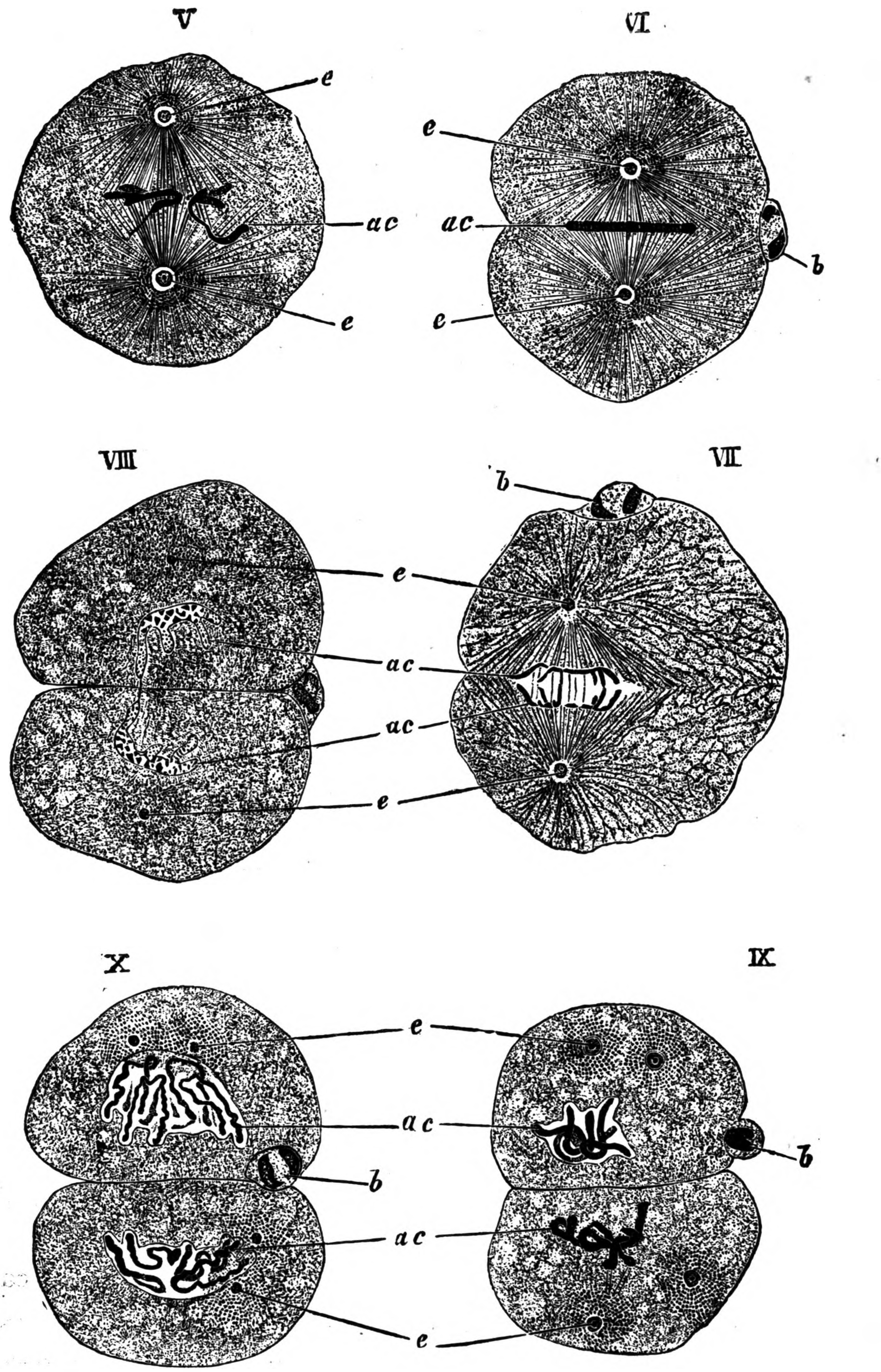


FIG. 15.—Diagram of the process of fertilisation in *Ascaris*. (After Boveri.)

a, female pronucleus; *b*, polar bodies; *c*, sperm pronucleus; *d*, sperm-cap; *ac*, chromosomes of united female and male pronuclei (*a* and *c*); *e*, centrosomes; fine (archoplasmic) threads radiating from the centrosomes. I–V show union of paternal and maternal chromosomes; VI shows equatorial plate of segmentation nucleus; VII–X show the division into the two first cleavage-cells or blastomeres.

into dwarf, but normal, larvæ. In these, as T. H. Morgan (1895) afterwards showed, the nuclei contain *only half the normal number of chromosomes*, having had only a sperm-nucleus to start with.

Interesting as this was, Boveri's further experiment was yet more striking. He fertilised the enucleated egg-fragments of one species of sea-urchin (*Sphærechinus granularis*) with spermatozoa of another species (*Echinus microtuberculatus*), and obtained in a few cases dwarf larvæ (plutei), which showed, except as regards size, the paternal characters only. Therefore he concluded that the nucleus is the exclusive bearer of the hereditary qualities, for it seemed from the experiment that the enucleated maternal cytoplasm had remained without specific influence.

It is admitted by Boveri himself that further experiments are necessary, and it must be granted also, as has been pointed out by Seeliger, Morgan, and Driesch, that in cases of hybridism, as in Boveri's experiment, there may be a marked illustration of what is called unilateral or preponderant inheritance. Most hybrid Echinoderm larvæ show maternal characters only, some show paternal characters only, some show both. There is also much individual variability. Thus Boveri's famous experiment affords no secure basis for argument.

5. *Additional Arguments.*—Further evidence of the importance of the chromosomes may be found in the fact that the number throughout any given organism is usually the same, except in the reduced gametes which have half the normal number.

Furthermore, in the history of the gametes the chromosomes are distributed in a way that corresponds to the distribution of hereditary characters in Mendelian inheritance.

Finally, one of the steps of modern advance is the proof (De Vries, Gates, T. H. Morgan, and others) that definite structural changes in the body of an organism are correlated with definite changes in the chromosomes of the fertilised egg-cell.

Another argument may be found in the fact that in some cases the sex of the offspring seems to depend on whether the egg is fertilised by a spermatozoon with an extra "accessory chromosome" or by a spermatozoon without this.

Generally accepted Conclusion.—The general conclusion from the foregoing and other arguments may be illustrated by two or three quotations from recognised authorities. Prof. O. Hertwig says:

"The female nuclear material transmits the characters of the mother, the male nucleus those of the father, to the offspring." Prof. Strasburger says for higher plants: "The process of fertilisation depends upon the union of the sperm-nucleus with the nucleus of the egg-cell; the cell-substance (cytoplasm) does not share in the process; the cell-substance of the pollen-grain is only the vehicle to conduct the generative nucleus to its destination." Prof. Weismann says: "We can hardly ascribe to the body of the ovum a higher import than that of being the common nutritive basis for the two conjugating nuclei."

Criticism.—1. "The life of a complex multicellular organism certainly depends upon the inter-relations and inter-actions of many parts; the life of a cell apparently depends upon the inter-relations

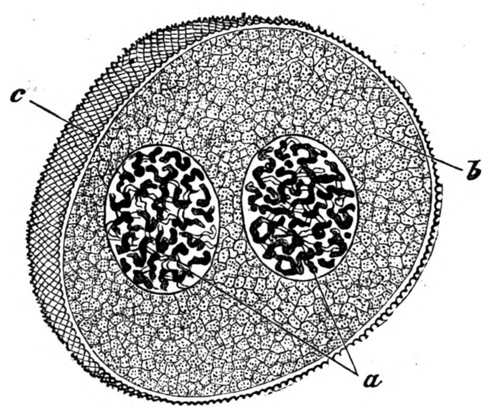


FIG. 16.—A pollen grain. *a*, the two nuclei, with their chromosomes; *b*, the general protoplasm; *c*, the outer wall. (From Carnoy.)

and inter-actions of different parts of the cellular organisation, especially on the give-and-take between nucleoplasm and cytoplasm; and it is not unlikely that life itself—*i.e.* vital activity or function—may depend upon the inter-relations and inter-actions of a number of complex substances, *none of which could by itself be called alive.* Just as the secret of a firm's success may depend upon a particularly fortunate association of partners, so it may be with vitality." * "We are compelled by the most stringent evidence to admit that the ultimate basis of living matter is not a single chemical substance, but a mixture of many substances that are self-propagating without loss of their specific character." † Holding firmly to this view,

* J. Arthur Thomson, *Science of Life*, p. 115 (London, 1899).

† E. B. Wilson, *The Cell in Development and Inheritance* (1st ed., 1896).

which we have elsewhere expressed, that life is a function of inter-relations, we confess to hesitation in accepting without saving clauses any attempt to call this or that part of the germinal matter the exclusive vehicle of the hereditary qualities.

2. The sperm-nucleus brings with it into the ovum a little cytoplasm, and it is also accompanied by the minute central corpuscle or centrosome, which seems to play an important part in regulating the mechanism of cleavage. It may be that the minimal quantity of cytoplasm is also important, though we cannot trace its behaviour as we do that of the centrosome. Strasburger says that if it were important there would be more of it, but in these matters size and mass seem of small moment; the little cytoplasm there is may act like the little leaven which leavens the whole lump. It seems in this connection very desirable that the experiments which have been begun (Piéri and Winkler) of extracting a ferment ("ovulase") from seminal matter and using it as a fertilising agent, should be confirmed or confuted.

3. In Loeb's experiments unfertilised sea-urchin's eggs developed into complete and normal larvæ; the sperm-nucleus was dispensed with. In Delage's experiments non-nucleated fragments of the ova of sea-urchin, worm, and mollusc were fertilised and developed into normal larvæ; the ovum-nucleus was dispensed with. But it must be noted carefully that in both cases there was *a* nucleus present.

4. Hickson (1907) has argued forcibly in support of the view that "for the present at any rate we can only say that the germ-cells as a whole, and not any special part, are responsible for the transmission of heritable characters from generation to generation." He suggests speculatively that the more plastic characters may be transmitted mainly by the cytoplasm and the rigid characters by the nucleus. In his criticism he refers to cases where chromosomes are quite indistinct in the gametes, to the importance of cytoplasm-fusion in the conjugation of some Protozoa, to the experiments of Herbst and Fischel on hybridisation in Echinoderms, which indicate the importance of the cytoplasm of the ovum in transmitting characters, and to other sets of facts which indicate the danger of exaggerating the importance of the chromosomes. The observations of Godlewski are also strongly suggestive of the importance of the cytoplasm, as well as the nucleus, in inheritance.

5. Bateson (1907) has pointed out that if the chromosomes were

the bearers of hereditary characters, we should expect some degree of correspondence between the differences distinguishing the types and the visible differences of number or shape distinguishing the chromosomes. Moreover, if the chromosomes were the chief governors of structure we should expect to find greater differences between them in different tissues of the same body.

6. No one has protested more clearly and vigorously than Guyer (1909, 1911) against "the inordinate importance which has been attributed to the chromosomes as vehicles of heredity." He points out, for instance, that there is definite experimental evidence of the great importance of the ovum-*cytoplasm*, and argues that "the number and arrangement of the chromosomes in a given species are the effects of the fundamental constitution of a given kind of living matter, rather than that they stand in a specifically causal relation to such constitution." "Heredity is the problem of the handing-on of metabolic energies already established, rather than of the transmission of a series of determinative units which create a wholly new organism." "This much is certain; no chemical, physiological, or morphological evidence is yet extant which places the hereditary factors wholly within the chromosomes." It seem highly probable that the chromosomes "control the velocities in cell-chemistry" by supplying the proper amounts and kinds of ferments which act on a series of fundamental cell-constituents that are largely common to both egg and sperm.

Perhaps then the safest conclusion at present is that the chromosomes, *along with other germ-cell constituents*, "stand in some definite causal relation to adult characters."

In T. H. Morgan's *Physical Basis of Heredity* (1919) a convinced statement will be found of the view that the main vehicles of the hereditary qualities are the chromosomes of the nuclei of the germ-cells. These chromosomes contain the differentiated areas (genes or factors) which are causally connected with the development of certain characters. But the cytoplasm of the egg-cell may contain hereditary plastids and building materials of importance; and in any case a germ-cell is a unity like a firm.

CHAPTER III

HEREDITY AND VARIATION

"The organic world as a whole is a perpetual flux of changing types."—
FRANCIS GALTON.

"Inheritance and variation are not two things, but two imperfect views of a single process."—W. K. BROOKS.

"Variation and inheritance are, at present, one fundamental mystery of the vital unit."—KARL PEARSON.

§ 1. *Persistence and Novelty.*
§ 2. *The Tendency to Breed True.*
§ 3. *Different Kinds of Organic Change.*
§ 4. *Classification and Illustration of Variations.*
§ 5. *Fluctuating Variations.*
§ 6. *Discontinuous Variations.*
§ 7. *De Vries on Fluctuations and Mutations.*
§ 8. *Causes of Variation.*

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§ 1. *Persistence and Novelty*

CLOSE observers of the relation between successive generations in mankind, or among plants and animals, are at one in recording two distinct impressions,—on the one hand, of persistent hereditary resemblance, on the other hand, of variability. Oftenest we are first impressed by the remarkable homogeneity which obtains from generation to generation, but as we get to know the organisms better we become aware of individual traits standing out against the background of general similarity. Or it may be that, with the partiality of parents, our first

impression is of the novelty and individuality of our children, and only later do we recognise in those, who seemed so original, a re-incarnation of our average selves. Oftener, perhaps, it will be discovered that the resemblance in habits of mind and body is purely *mimetic*, and that the idiosyncrasies which were really present, as buds at least, have been pruned off both for good and for ill by the hook of criticism, or driven into latency —like "sleeping-buds"—by mis-education or lack of appropriate stimulus.

Like Tends to Beget Like.—The hereditary relation is such that offspring are on the whole like their parents, but the degree of this likeness varies within wide limits. Indeed, the discrepancies are often very conspicuous, and we can understand how Prosper Lucas, one of the early students of inheritance (1847)—careful and scholarly according to his lights—imagined a metaphysical entity, which he called "*l'innéité*" and opposed to "*l'hérédité*," the former originating what is new, the latter conserving what is old. In modern phraseology, the occurrence of variations is a fact of life so general that we must replace the adage "Like begets like" with the more cautious statement "Like tends to beget like."

The popular adage "Like begets like" is often true as a general statement. Offspring are often so like their parents that even the scientific observer cannot tell one from the other. In other words, the species "breeds true." But the more intimate our acquaintance with organisms becomes, the more plainly do we detect individual peculiarities, and we have to change the adage to "Like tends to beget like." On the whole it is true that average parents have average offspring, that exceptional parents have exceptional offspring. Like tends to beget like. Yet it is well known that, for instance as regards stature, the tall do not always beget the tall, or the small the small, so that we have to broaden the most general "fact of inheritance" still further, and say that the average character

attained by the individuals of one generation tends to be very nearly the same as the average character of the preceding generation. This is the broad fact of specific inertia.

A False Antithesis between Heredity and Variation.—Much obscurity of thought has been due to the false antithesis between heredity and variation. When we say that like tends to beget like, that offspring tend to resemble their parents and ancestors, we are stating a fact of life. But when we speak of an opposition between a force or principle of heredity, securing resemblance between offspring and their parents, and a tendency to variability which makes offspring different from their parents, we are indulging in verbiage. Heredity, as we have repeatedly said, is the relation of genetic continuity between successive generations, and it is such that while many characters seen in parents persist in their offspring, there is also in most cases a distinct individuality in these offspring. Heredity is a condition of evolution, a condition of inborn variations; it is just a name for the reproductive or genetic relation between parents and offspring. The inheritance which was expressed in the development of the parent may be almost identical with the inheritance which is expressed in the development of the offspring, but in most cases the inheritance does not persist in this intact way from generation to generation, and then we speak of variation. The contrast is not between heredity and variation, but between inertia and change, between continuity or persistence and novelty or mutation, between completeness of hereditary resemblance and incompleteness of hereditary resemblance.

As Prof. W. K. Brooks says (1906, p. 71): "Living beings do not exhibit unity and diversity, but unity in diversity. These are not two facts, but one. The fact is the individuality in kinship of living beings. Inheritance and variation are not two things, but two imperfect views of a single process."

§ 2. *The Tendency to Breed True*

Relative Stability of Specific Characters.—Belonging as we do to a race which seems to have varied very slowly within historic times, we have not far to seek for good examples of what is the biggest fact of inheritance—the stability of specific characters throughout a long series of generations. If we exclude monstrosities due to arrested development and the like, if we set aside the numerous malformations and deformations induced on the bodies of individuals by peculiarities of function and environment, the stability of the essential human characteristics for many millennia is obvious. This racial inertia, which holds in some measure at least for mental characteristics, is at once the hope and the despair of the social reformer.

If we pass from general specific characters to those of particular races, we read the same story. Not only do the salient characteristics of the skull persist within a narrow radius of variability, but the same is true of minor features: the oblique eyes of the Japanese, the oval face of the Esquimaux, the woolly hair of the Negro and the Jewish nose.

Conservative Types of Organisation.—But the persistence of structural and mental characters as illustrated in mankind is but a tale of yesterday when compared with the persistence of type exhibited by many animals which have lived on apparently unchanged for many millions of years. Whatever may be true in regard to the soft parts, of which no record remains, there seem to be no differences in hard parts distinguishing the *Lingula* of to-day from those of the Silurian ages; and there are other instances of what are sometimes called "living fossils." The reasons for such remarkable persistence do not now concern us, but the fact that structural characters established millions of years ago are reproduced with exactness at the present moment does.

Persistent Peculiarities in Families.—Not less striking than the long persistence of specific and stock characters is the fact that offspring frequently reproduce the *individual* peculiarities—both normal and abnormal—of their parents or ancestors. A slight structural peculiarity, such as a lock of white hair or an extra digit, may persist for several generations. A slight functional peculiarity, such as left-handedness, has been recorded for at least four generations, and colour-blindness for five. The strong under-lip of the Hapsburgs persisted for six centuries. There are endless illustrations of the fact that a pathological diathesis—rheumatic, gouty, neurotic, or the like—may persist and express itself similarly, even in spite of altered conditions of life, throughout many generations. And what is true of bodily characteristics is not less true of mental peculiarities: as to this, popular impressions and the careful investigations of Galton and others are in agreement. We think at once of cases like the Bachs, the Bernouillis, the Darwins!

§ 3. *Different Kinds of Organic Change*

It may conduce to clearness if we think over the different kinds of changes which occur in organisms.

1. **Metabolism.**—All living creatures are, as it were, whirlpools in the universal ocean of matter and energy. They are continually changing as they live. Streams of matter and energy pass in and out. Organisms are animate systems which transform matter and energy in a characteristic way which we call living. Their physical basis is continually undergoing disruption and reconstruction; it breaks down and is built up again, it wastes and is repaired, it runs down and is ever being wound up again—until the arrears of imperfect recuperation become so serious that the organism dies, or until some fatal accident occurs. The chemical and physical changes involved in living are summed up

in the term metabolism, the two aspects of which—constructive and disruptive—are called anabolism and katabolism.

2. **Cyclic Changes.**—An equally familiar fact is that organisms pass through a series of changes. The fertilised egg undergoes cleavage, the resulting cells grow and differentiate, an embryo is formed, and gradually—often by circuitous paths—a miniature form of the adult creature is attained. Out of apparent simplicity an obvious complexity results. Growth still continues, often punctuated by resting periods, often rhythmic and

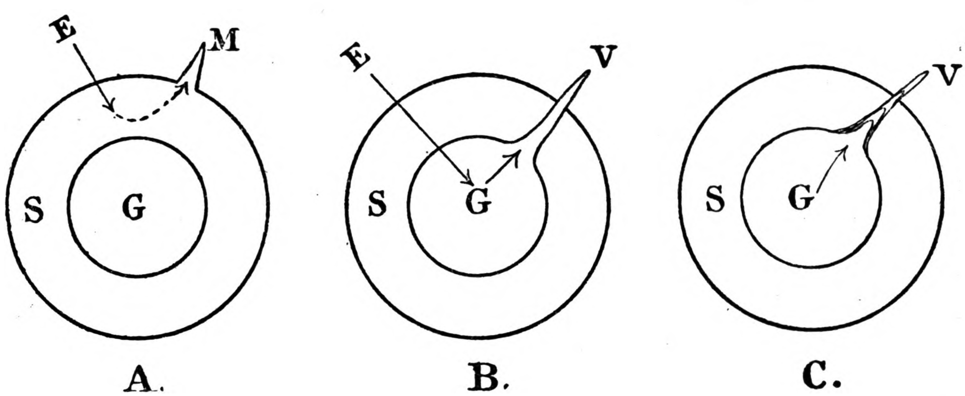

FIG. 17.—Diagram illustrative of variation and modification.

S, the soma or body; G, the germinal material; E, an environmental change.
A, an environmental change acting on the body directly evokes a modification (M).
B, an environmental change, without modifying the body directly, acts as a stimulus on the germ-plasm, and is followed by a variation (V).
C, a variation (V) arises from some germinal change which cannot be causally connected with any particular environmental change.

expressible in complex curves, often interrupted by peculiar crises. Quickly or slowly the organism passes from youth through adolescence to maturity, to its limit of growth and its reproductive maturity. Quickly or slowly thereafter it sinks on a down-grade towards death. As the old naturalists said, from one period of vita minima the creature rises to a period of vita maxima, and sinks back again into a vita minima which

dwindles to a vanishing point. It is characteristic of organisms to pass through a series of cyclic changes.

3. **Changes involved in Functioning.**—As contrasted with inanimate systems, organisms are characterised by their power of *effective response* to environmental stimuli. A living creature's responses tend towards self-preservation or species-preservation. Though they may fail, the reactions are primarily and fundamentally effective. And these functionings or effective responses necessarily involve changes in the system. They involve wear and tear, and leave more or less discernible results. Normally, however, the results, known as fatigue-effects and the like, are obliterated by nutrition, rest, and other forms of recuperation. In the study of an intricate structure, like a bee's brain, it is possible to arrange on an inclined plane the changes which are normally obliterated by a night's rest, the changes which require prolonged recuperation before they disappear, and the changes which cannot be recovered from—which accumulate until the bee dies a natural death.

4. **Temporary and Individual Adjustments.**—In addition to the inherent primary power of effective response, organisms have different degrees of plasticity. They can adjust their reactions to novel conditions. They can "try" first one mode of reaction and then another, finally persisting in that which is most effective. Even the unicellular Infusorians do this. How much of this plasticity is primary, or inherent in the very nature of living matter, how much of it is secondary and wrought out by Natural Selection in the course of ages, must remain in great measure a matter of uncertainty. Each case must be judged on its own merits. It is certain that many unicellular organisms are very plastic, and it seems reasonable to suppose that as differentiation increased, restrictions were placed on the primary plasticity, while a more specialised secondary plasticity was gained in many cases, where the organisms lived in environments liable to frequent vicissitudes. It is convenient to use the

term "accommodations" for the frequently occurring individual adjustments which many organisms are able to make to new conditions.

5. **Modifications.**—Besides being plastic, organisms are modifiable: that is to say, in the course of their individual life they are liable to be so impressed by changes in surrounding influences and by consequent changes in function that, as a direct result, modifications of bodily structure or habit are acquired. Modifiability is the capacity of registering the direct results of changed function or of changed environment. "Modifications" may be defined as structural changes in the body of an individual organism, directly induced by changes in function or in environment, which transcend the limit of organic elasticity and persist after the inducing conditions have ceased to operate. They are often inconveniently called "acquired characters." They are not proved to be transmissible as such or in any representative degree, but they are often adaptive and individually very valuable. They are distinguishable from temporary adjustments or accommodations on the one hand, and from inborn variations on the other.

6. **Inborn Variations.**—Finally, when we subtract from a total of "observed differences" between members of the same species all that can be described as accommodations and modifications, we find a large remainder which we must sharply define off as *variations.* We cannot causally relate them to peculiarities in habit or in surroundings; they are often distinct at birth or hinted at before birth; and they are rarely alike even among forms whose conditions of life seem absolutely uniform. They may be large or small in amount, fluctuations or freaks, progressive or retrogressive—that is a matter for further analysis—but they agree in having a germinal origin. They are endogenous, not exogenous; they are born, not made; and they are more or less transmissible, though they are not

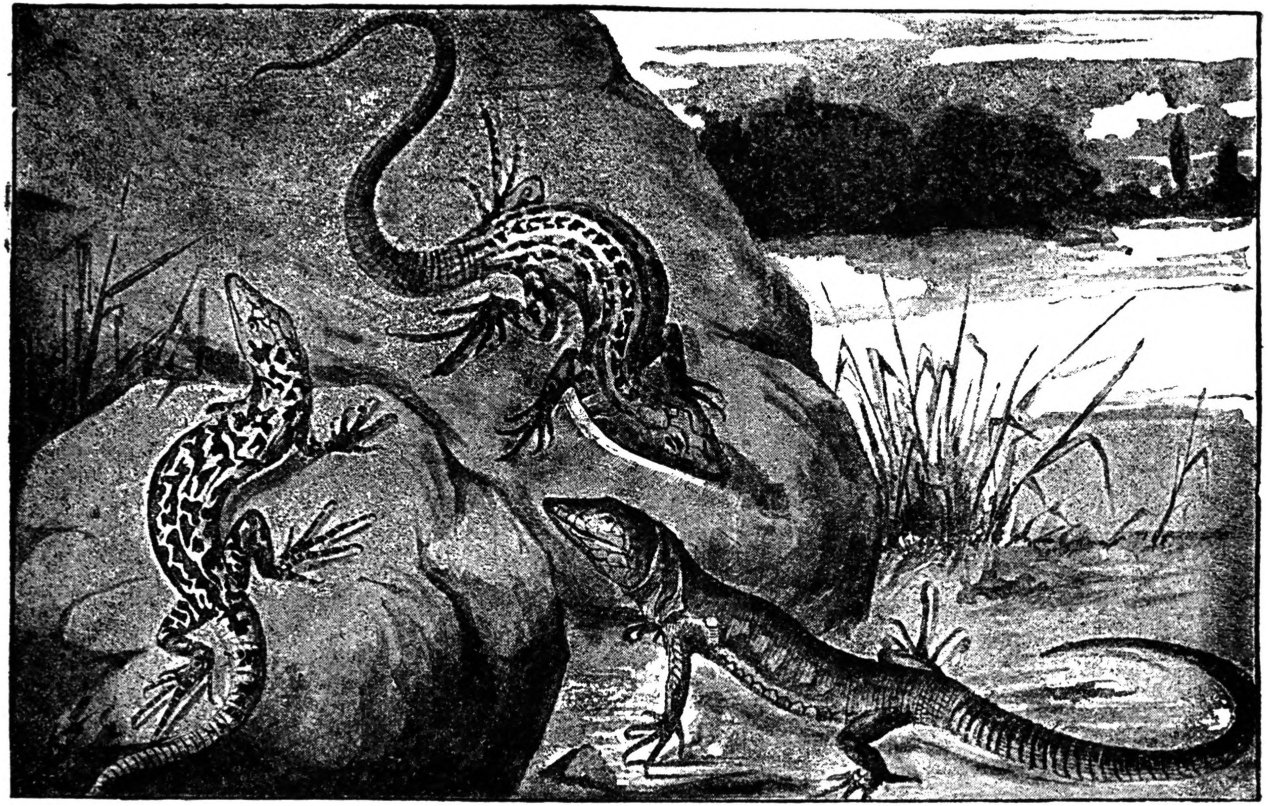

FIG. 18.—The wall-lizard (*Lacerta muralis*), three differently coloured and marked varieties of the same species. (Compiled from Eimer.)

always transmitted. They form—at least some of them form—the raw material of organic evolution.

§ 4. *Classification and Illustration of Variations.*

"Variation."—It is a common confession of naturalists that a label is a necessary evil. A collection without labels is a contradiction in terms, and yet the label is often a full-stop to investigation. This is true in regard to the concrete; it is more lamentably true in regard to the abstract. Thus the label "Variation" has been a great hindrance to progress.

As Mr. Bateson says (1905, p. 575): "The indiscriminate confounding of all divergences from type into one heterogeneous heap under the name 'Variation' effectually concealed those features of order which the phenomena severally present, creating an enduring obstacle to the progress of evolutionary science. Specific normality and distinctness being regarded as an accidental product of exigency, it was thought safe to treat departures from such normality as comparable differences: all were 'variations' alike."

All organic changes imply some incompleteness in the hereditary resemblance—a little more of one character, a little less of another, or the occurrence of some feature which deserves to be called distinctly "new." Both variations and modifications may cause this incompleteness in the hereditary resemblance; an apparently similar condition may result from two different processes of change. But the variation has a germinal origin, is blastogenic, is not directly dependent on the external conditions of life, is endogenous, and is transmissible; while the modification has a somatic origin, is the direct result of functional or environmental influence, is exogenous, and, so far as we know at present, is not as such transmissible.

Classification.—There are many different ways of classifying these variations which form the raw material of evolutionary change.

a. If we attend to the *nature of the change*, we may distinguish "*meristic*" variations—*e.g.* in the number and proportions of parts, from "*substantive*" variations of a qualitative sort—*e.g.* change in colour.

β. If we attend to the *direction of the change* in successive generations, we may distinguish "definite" variations, which occur along one line (like stages in normal development), from "indefinite" variations, which "fluctuate hither and thither with no uniformity in the course of generations."

Many evolutionists have maintained that there is good reason for believing in definite or determinate variation along particular lines, as if certain organisms had an inherent bias to change in certain parts and not in others, in certain directions and not in others, just as certain inorganic substances can crystallise in different forms but only within strict limits. It is possible to arrange a series of species A, B, C, D, E, F, in such a way that they suggest progressive definite variation along a particular line, and it seems not unlikely that this kind of evolution may sometimes occur. Moreover, along quite different lines of evolution we find evidence that the same kind of step has been taken independently, over and over again. This suggests that the possibilities of variations may be limited and defined by deep-rooted constitutional conditions or physiological alternatives. But the weakness of the argument lies in the almost insuperable difficulty of deciding whether the apparent definiteness is not the result of the primary action of selection which eliminates divergent variants at early stages—nipping idiosyncrasies in the bud—or which may have established a bias in previous generations. In conditions of rigid elimination the lines of variation will naturally tend to become more and more restricted.

γ. If we attend to *the amount of the change* from one generation to the next, we may distinguish minute fluctuations about a mean, which are connected by intergrades, from sudden

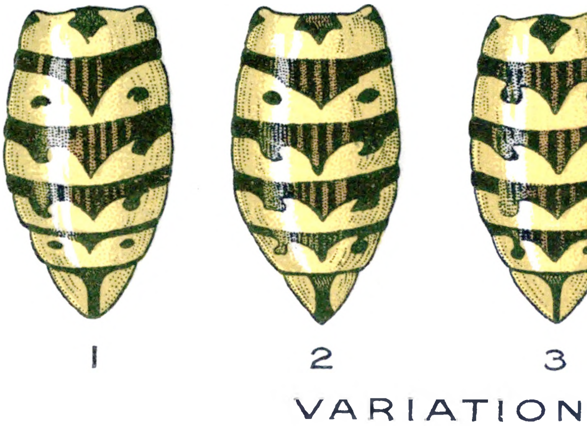

Fig.19.

FIG. 19.—Some of the numerous variations in the pattern of the abdomen in the yellow jacket Wasp. [After Kellog and Bell.]

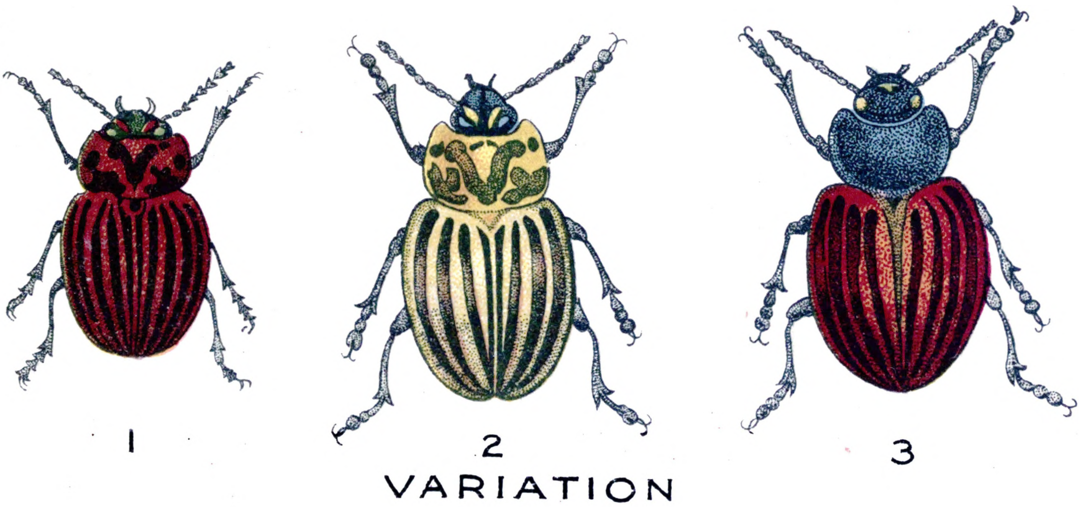

Fig.20.

FIG. 20.—"Mutations" or rapidly developing large inheritable variations in *Leptinotarsa multitæniata*. The type of the species (2) and its extreme mutants *rubicunda* (1) and *melanothorax* (3). [After W. L. Tower.]

[*Facing p.* 76

"sports" which reach a new position of organic equilibrium as if by a leap. This is the contrast between "continuous" variations small in amount, and "discontinuous" or "transilient" variations in which a considerable step is taken with apparent suddenness, without the occurrence of intermediates.

The term variation, used concretely to denote an organic peculiarity or idiosyncrasy, is obviously a relative term, implying some standard of comparison. It is a deviation from the parental type, a divergence from the mean of the stock. Thus there are different degrees, or perhaps even different kinds of discontinuity.

In many cases, a variation may be described as simply an incompleteness in the inheritance or in the expression of the inheritance. The divergence from the norm is due to the suppression or inhibition of some character. This may be illustrated by a perfectly white (albino) baby, born to almost coal-black parents.* If such a form became the founder of an albino race, as in the case of rats and mice, we should be justified in concluding that the particular material organisation which eventually leads to the deposition of pigment in the body had somehow dropped out of the inheritance. If the albinism was in no respect transmitted to the next generation, we should be justified in concluding that the structural arrangements which lead on to pigmentation had simply been hindered from finding their normal expression in development.

A minus variation like albinism may be described as due to an incompleteness in the inheritance or in the expression of the inheritance, but there are other variations which must, so to speak, bear the plus sign, for they involve the augmentation or exaggeration of a character. Plus variations of this sort have

* "Its father and mother were horrified; their friends and relations, in fact all the villagers, were called to examine and criticise it. Why such surprise? Why such commotion? The answer is self-evident: the law of heredity had been broken."—R. W. Felkin. The vulgar mind is always impressed by size and quantity; big deviations strike the imagination, and the normal occurrence of small deviations is forgotten.

been taken advantage of in breeding sheep with long fleece, Japanese cocks with tails ten feet long, "wonder horses" with manes reaching the ground, and so on.

But the offspring is sometimes so different from the parent that we cannot describe its peculiarity as an incompleteness in the expression of the normal inheritance, or as an exaggeration of parental or ancestral traits. It is sometimes a new pattern, a fresh departure, with what one might call organic originality. It is more than a discontinuous variation. It seems to have passed suddenly into a new position of organic equilibrium, where it has not only individuality, but a distinctively novel individuality. These distinctive novelties, which arise brusquely, are often included in the conception of "mutations."

§ 5. *Fluctuating Variations*

When we examine a number of individuals of the same species we usually find that they differ from one another in detail. Some of the observed differences may be modificational or due to differences of nurture, but it is often possible to abstract these from differences due to hereditary nature. Thus, when we collect a large number of specimens of the same age from the same place at the same time, we often find that no two are exactly alike. They have peculiarities of germinal origin—or, in other words, they show *fluctuating variations*. The characteristic feature of these fluctuations is that they are *continuous*, *i.e.* connected by intergrades, and that they can be arranged in a gradual series (a curve of frequency) on each side of a mode.

To construct such a curve (let us say of variation in stature), take a base line, and divide it into equal parts, each to represent a unit of measurement, say an inch. From a middle division of this base line erect an ordinate to represent by its length the number of those individuals whose stature is found to be the most frequent. On each side of this, from their appropriate

divisions on the base line, erect ordinates representing by their length the number of individuals of each stature, the lower statures to the left, the greater to the right. Now a line joining the tops of the ordinates will form a polygon or (if the divisions in the base line be quarters of an inch) a curve, which will show graphically *the distribution of variation in stature in the population measured.* If the curve is symmetrical on each side of the highest ordinate, *the mode*, it is called the "normal curve"; the average or *mean* coinciding with the "mode." If there are more variations on one side of the mode, the curve is "skew"; if there are two maxima or modes, the curve is "dimorphic"; and so on. In various ways, which are of great practical convenience, a *measure of variability* can be deduced from the steepness or flatness of the curve, and thus we can readily compare the variability of different characters, or of the same character in different groups and at different times. The curves, especially if made year after year, may show the direction in which the species is moving, perhaps the way in which selection is working, perhaps even that the species is splitting up into two subspecies.

One of the results of measuring large numbers of variations is to show that there is a relation between the amount of a deviation and the frequency of its occurrence. The greater the divergence from the average, the fewer instances are there. Measurements of a large number of soldiers gave Quetelet the following result, in which the upper line indicates the heights in inches, and the lower line the number of soldiers of each of these heights.

60,	61,	62,	63,	64,	65,	66,	67,	68,	69,	70,	71,	72,	73,	74,	75,
2,	2,	20,	48,	75,	117,	134,	157,	140,	121,	80,	57,	26,	13,	5,	3.

The general symmetry is plain, on each side of the most frequent condition, 67 inches, which is called the "mode."

Registration of Variations.—"The modern methods of statistics deal comprehensively with entire species, and with entire groups of influences, just as if they were single entities, and express the

relations between them in an equally compendious manner. They commence by marshalling the values in order of magnitude from the smallest up to the largest, thereby converting a mob into an orderly array, which, like a regiment, thenceforth becomes a tactical unit. Conceive each value to be represented by an extremely slender rod of proportionate length, and the rods to be erected side by side, touching one another, upon a horizontal base. The array of closely-packed rods will then form a plane area, bounded by straight lines at its sides and along its base, but by a flowing curve above, which takes note of *every one* of the values on which it is founded, however immense their multitude may be. The shape of the curve is characteristic of the particular group of values to which it refers, but all arrays have a family resemblance due to similarity of origin; they all drop steeply at one end, rise steeply at the other, and have a sloping back. An array that has been drilled into some such formation as this, is the tactical unit of the new statistics" (*Biometrika*, vol. i., 1901, p. 7).

Theory of Evolution by Selection of Fluctuating Variations.—It is certain that most offspring differ from their parents in many quantitative details. It is certain that when measurements are taken of a large number of individuals of the same species in reference to a particular character, the results, when plotted out, conform approximately to the normal curve of frequency. If measurements be taken in a subsequent generation there is a similar result, but the curve need not be precisely the same. The mode of the curve—*i.e.* the most frequently occurring dimension of the measured character, may change from one generation to another. It is usually believed that one of the ways in which this change can be effected is by natural selection. But to think of new species arising by slow changes of this sort is in many ways difficult, apart altogether from the fact that definite demonstration of the operation of selection has been rarely attempted.

(1) Such a character as a Roman nose is certainly heritable, though it is not always inherited. But we cannot speak so

definitely in regard to small quantitative variations. A tall father does not necessarily have tall children. Where the characters in which the two parents differ are such as readily blend, regression towards the mean of the stock will occur.

(2) Even with very thorough isolation—segregation of like individuals—and very consistent selection, it is doubtful whether a new race could be evolved from the cumulative increase of small quantitative variations, *e.g.* in stature or colour of hair. It is doubtful whether any domestic races have so arisen. It is not in this way that dwarf-races and giant-races have been formed. They arise from sudden discontinuous variations or mutations, which are often peculiarly heritable, which are anything but liable to be swamped by inter-crossing, and which sometimes exhibit Mendelian inheritance.

(3) The result of the gradual accumulation of small quantitative variations may be very important in a long time, just as a small sum may become large from interest accumulated for centuries; but it is difficult to believe that minute fluctuations in quantity would always have sufficient selective value to ensure their persistence.

There are several reasons why selectionists have restricted themselves so much to continuous variations as the raw material of evolution. (1) Until lately we have known comparatively little in regard to discontinuous variations or mutations. (2) It was hastily concluded that these changes were not likely to be transmitted—a generalisation in part due to preoccupation with teratological non-viable freaks. (3) In many cases related species can be arranged in a gradual series with intermediate forms linking the extremes.

Now, there is no need to hamper the Evolution Theory by restricting selection to minute variations. We know that sports, mutations, or discontinuous variations are frequent, and that they are remarkably stable in their hereditary transmission.

We know also that many domestic races have, as a matter of fact, arisen by sudden mutation.

As to the series of related species which may be often arranged as if on an inclined plane, two points should be noted: (1) that it is likely enough that some kinds of species, *e.g.* vegetative forms like Alcyonarians and Corals, may have evolved by minute steps, and (2) that although species are often connected by intermediate links it does not follow that these links are stages in the evolution. They may have been formed *after* the species to which they are theoretically supposed to give rise. We should remember Galton's warning, "If all the variations of any machine that had ever been invented were selected and arranged in a museum, each would differ so little from its neighbours as to suggest the fallacious inference that the successive inventions of that machine had progressed by means of a very large number of hardly discernible steps." Many facts now lead us to conclude that the Proteus *leaps* as well as creeps.

§ 6. *Discontinuous Variations*

One of the steps of progress in Evolution-lore since Darwin's day is the recognition of the frequency and importance of discontinuous variations—*i.e.* of organic changes which arise abruptly and not by a gradual series of steps. If dwarfs arise suddenly in a tall race, and are not mere modifications, they illustrate discontinuous variation of a quantitative sort. A hornless calf, a tail-less kitten, a short-legged lamb, a thornless rose, illustrate discontinuous *quantitative* variations of a *negative* kind. Giants, "wonder-horses," long-tailed Japanese cocks, merino-fleeced sheep, spine-covered holly leaves illustrate discontinuous *quantitative* variations of a *positive* kind. Sometimes the novelty cannot be readily expressed in quantitative terms—an entirely new colour turns up, the variant is immune to certain diseases to which the stock is susceptible, leaves become fasciated,

a tree becomes "weeping," a genius is born. When a new pattern of organisation or a new constitutional property turns up, we may speak of a discontinuous *qualitative* variation.

Historical Note.—The idea that organic changes might come about by leaps and bounds is not novel, though the evidence substantiating it is quite modern.

Some of the older evolutionists, such as Etienne Geoffroy St. Hilaire, believed in saltatory evolution, and were far from agreeing with Lamarck that Nature is never brusque.

Darwin also recognised that big steps may be taken suddenly—*e.g.* in the origin of large-crested Polish fowls, black-shouldered peacocks, short-legged Ancon sheep, but he thought that these discontinuous variations occurred rarely, and would be liable to be swamped by intercrossing. He relied rather on the action of natural selection on the small, continuous variations which are always forthcoming.

But the modern appreciation of the importance and frequency of discontinuous variations is mainly due to Bateson, who, in his *Materials for the Study of Variation* (1894), gave many instances of the sudden appearance of offspring which in some particular diverge widely and abruptly from their parents; and to De Vries, who has observed the occurrence of "mutations" in many plants, and has also followed them through generations, showing that they tend to breed true; and to Johannsen, who recognised the importance of *individual* new departures in starting stable "pure lines."

A Change of View.—Darwin and orthodox Darwinians relied in the main on the operation of selection on small individual variations—many of which are nothing more than quantitative fluctuations. If new adaptations and new discontinuous species arise in this way, the small variations must be heritable, the new character must be capable of cumulative increase by the persistent outcrop of similar variations generation after generation, the selection must be persistent and consistent, and a long time must be allowed.

Even when this theory is strengthened by subsidiary theories, *e.g.* as to the efficacy of isolation and germinal selection, it is more theoretically than practically convincing. It places such a heavy burden on the shoulders of Natural Selection that the idea of a leaping instead of a creeping Proteus has always been welcome.

But why are evolutionists now entertaining an idea—the importance of discontinuous variations—which Darwin considered and then rejected? The answer is that we now know of many instances of discontinuous variation in animals, and even more among plants, that we have some good evidence of these discontinuous variations or mutations "breeding true," and that we have in the theory of Mendelian inheritance a reason why a mutation which has once arrived should persist.

Some modern authorities go the length of saying that "mutations" form the sole raw material of evolution, and that "individual fluctuations" do not count at all. This seems an illustration of the common tendency to take up an extreme position in the enthusiasm of a new discovery. Because discontinuous variations are common and important it does not follow that continuous fluctuations are of no moment. Those "whose humour is nothing but mutation" confess that it is very difficult to distinguish between a small mutation and a large fluctuation. If the large fluctuation be heritable—which we may assume until it has been disproved—we confess that we do not see what is gained by trying to distinguish it from a small mutation.

The New View.—Dominated by the idea that "organisms are mere conglomerates of adaptative devices," and that these patents cannot but be the outcome of slow accumulation of minute fluctuations under the directive agency of selection, naturalists have paid little heed to the open secret that the living creature is inherently a Proteus suddenly and discon-

tinuously passing from one guise to another by transilient variation.

Mr. Bateson (1905, p. 577) notes that Marchant in 1719 was the earliest to comment on the suggestiveness of sudden changes, such as he saw in plants of *Mercurialis* with laciniated and hair-like leaves which for a time established themselves in his garden. He suggested that species may arise in like manner. "Though the same conclusion has appeared inevitable to many, including authorities of very diverse experience, such as Huxley, Virchow, F. Galton, it has been strenuously resisted by the bulk of scientific opinion, especially in England.

"Upon whatever character the attention be fixed, whether size, number, form of the whole or of the parts, proportion, distribution of differentiation, sexual characters, fertility, precocity or lateness, colour, susceptibility to cold or to disease—in short, all the kinds of characters which we think of as best exemplifying specific difference, we are certain to find illustrations of the occurrence of departures from normality, presenting exactly the same definiteness elsewhere characteristic of normality itself. Again and again the circumstances of their occurrence render it impossible to suppose that these striking differences are the product of continued selection, or, indeed, that they represent the results of a gradual transformation of any kind. Whenever by any collocation of favouring circumstances such definite novelties possess a superior viability, supplanting their 'normal' relatives, it is obvious that new types will be created."

Heredity and Evolution.—Mr. Bateson has done good service in exposing to ridicule the prevalent misconception that domesticated races are "so many incarnations of the breeder's prophetic fancy." "Except in recombinations of pre-existing characters—now a comprehensible process—and in such intensifications and such finishing touches as involve variations which analogy makes probable, the part played by prophecy is small.

Variation leads ; the breeder follows. The breeder's method is to notice a desirable novelty, and to work up a stock of it, picking up other novelties in his course—for these genetic disturbances often spread—and we may rest assured the method of nature is not very different " (1905, p. 578).

This is obviously a very important change of view, though it is also in a way a return to what Darwin himself taught. "*Variation leads ; the breeder follows.*" But more than that : Variation leads by leaps and bounds. As Mr. Bateson says, let the believer in the efficacy of selection operating on continuous fluctuations try to breed a white or a black rat from a pure strain of black-and-white rats by choosing for breeding the whitest or the blackest ; or to raise a dwarf (" Cupid ") sweet pea from a tall race by choosing the shortest. It will not work. Variation leads and selection follows.

Illustrations of Discontinuous Variation

Wonder Horses.—The so-called wonder-horse " Linus I." had a mane eighteen feet long and a tail twenty-one feet long. The parents and grandparents had unusually long hair. This seems a good illustration of a " sport " or discontinuous variation which not only persisted for several generations, but increased very rapidly.

Shirley Poppies.—The well-known Shirley Poppies arose from a single discontinuous variation, which may have occurred often before Mr. Wilks saved it from elimination and made it the ancestor of a prolific and distinctive stock.

Star Primrose.—The graceful star primrose (*Primula stellata*) arose as a sport from the conventional Chinese primrose, and was raised by Messrs. Sutton into a favourite stock. It had been thrown off before as a sporadic variety over and over again, but was " promptly extirpated because repugnant to mid-Victorian primness."

The Moth Amphidasys.—Some sixty years ago in the urban conditions of Manchester the black variety *doubledayaria* of the moth *Amphidasys betularia* found its chance, and soon practically superseded the type in its place of origin, extended over England, and appeared even in Belgium and Germany (Bateson, 1905, p. 577).

The Common Jelly Fish.—A good case of abundant discontinuity in variation is furnished by the common jelly-fish *Aurelia aurita*, whose sports have been studied by eight or more observers, from Ehrenberg (1835) onwards. Its parts are normally in multiples of 4 (4 equal areas in the radially symmetrical disc, 4 oral lips, 4 genital organs, 16 radial canals, 8 marginal sense-organs or tentaculocysts); but numerical sports are very common. These are sometimes irregular, *e.g.* when the radial symmetry of the disc is lost; but they are oftener quite symmetrical, *e.g.* when the animal has 2 genital organs, 2 oral lobes, 8 radial canals, and 2 marginal sense-organs.

In studying *Aurelia aurita* at Plymouth, Browne (1895) found that out of 1515 young forms (ephyræ) 21·4 per cent. had more or fewer than 8 marginal sense-organs, and that out of 383 adults 22·8 per cent. were similarly affected. The figures seem to show that the abnormal forms survive quite as well as the normal forms, yet there is no evidence that the sports were more numerous in 1895 than when Ehrenberg studied them sixty years before. In other words, although a plentiful crop of brusque variations is being continually supplied by this plastic form, there is no hint of the origin of a new race. (Bateson, 1894, p. 428.)

The Case of Pseudoclytia.—Although the numerous discontinuous variations of *Aurelia aurita* do not suggest that any new race is at present arising, it is possible to find an analogous case where it does seem that we have to do with a species newly arisen, or still in process of being established. A. G. Mayer found at the Tortugas, Florida, large numbers of a medusoid

or swimming bell—*Pseudoclytia pentata*—a leptomedusan belonging to the family Eucopidæ. "It differs from all other Hydromedusæ in that it normally possesses 5 radial canals, 5 lips, and 5 gonads, all 72° apart, instead of 4 of these various organs 90° apart, as in other Eucopidæ." In the structure of its tentacles, otocysts, gonads, and manubrium, in the general shape of its bell, and the arrangement of its tentacles and otocysts, it is so closely similar to *Epenthesis folleata*, that it seems safe to conclude that the former has been derived from the latter or from some closely allied species. The two forms are somewhat different in colour and slightly different as to the position of the gonads, but the resemblance is exceedingly close, and no one can suppose that a medusoid with 5 radial canals is a primitive form. As there are pentamerous variants of *Epenthesis folleata* and tetramerous variants of *Pseudoclytia pentata*, we are not aware of any case which more cogently suggests the evolutionary interpretation. As Mayer says, "*P. pentata* may be called 'a new race' in the sense that it is evidently derived from *Epenthesis*, and departs from the quadratic arrangement of organs, which is almost universal among Hydromedusæ. It is remarkably variable, and its great commonness attests to its successfulness in the struggle for existence" (Mayer, 1901, p. 20).

To obviate misunderstanding, it may be observed that by the term "newly arisen" which Mayer uses in reference to *Pseudoclytia pentata*, he means simply that "it has departed widely from the fundamental type of all other Hydromedusæ, and that it is apparently derived from a genus (*Epenthesis*) which is itself quite highly differentiated. It is, therefore, 'new' in the sense that it cannot be a primitive form, although we have no means of determining how long a time it may have been in existence" (Mayer, 1901, p. 8).

While we cannot exactly demonstrate that *Pseudoclytia pentata* arose by discontinuous variation from *Epenthesis folleata*, or some closely allied form, the evidence in favour of that interpretation

is exceedingly strong. It is interesting further to notice that "the newly-arisen species" is very successful as regards numbers, and that its variations have a strong family resemblance to those of its supposed ancestor, and are yet more abundant. In regard to its more abnormal variants, Mayer observes that they are handicapped by their loss of symmetry, for some are neither radial nor bilateral, and by a reduction of fertility even in cases where the number of gonads has been increased to six or seven.

The evidence from Medusæ and Medusoids is sufficient to show

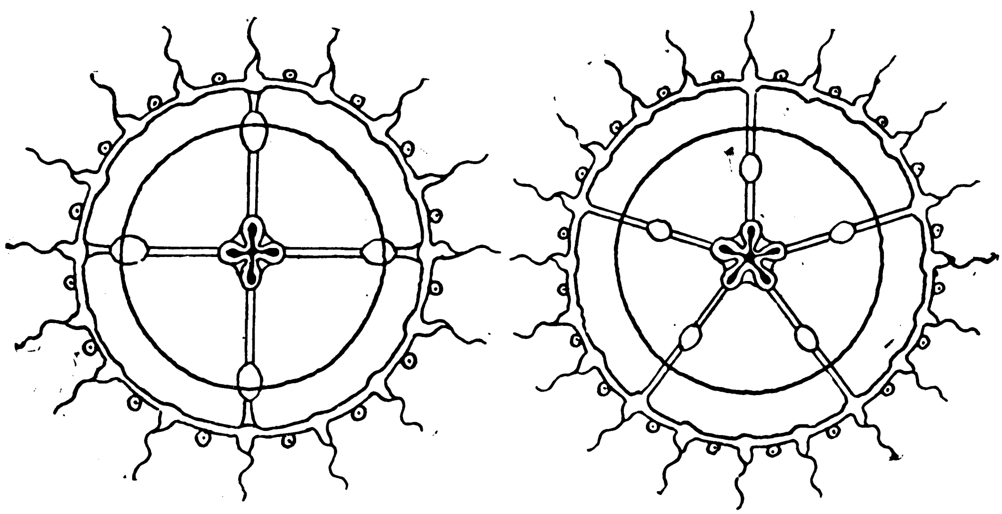

FIG. 21.—Mutation in Medusoids (after A. G. Mayer). The figure to the left is an oral view of *Epenthesis folleata.* The figure to the right is an oral view of *Pseudoclytia pentata.*

that discontinuous variations may occur in large numbers, that similar brusque changes may occur year after year, that there is sometimes a strong family resemblance in the variations of related forms. In some cases (*e.g.* in regard to *Aurelia aurita*) we are not in a position to say that anything has come of the abundant crop of discontinuous variations; in other cases (*e.g.* the very abnormal forms of *Pseudoclytia pentata*) the discontinuity has gone too far, as shown by the reduction of fertility and the entire loss of symmetry; while, thirdly, from the relationship of *Pseudoclytia pentata* to *Epenthesis folleata*, we are led to conclude that one species may arise from the discontinuous variation of another.

§ 7. *De Vries on Fluctuations and Mutations.*

Professor Hugo de Vries is one of the foremost of Darwin's intellectual heirs, with a rich endowment of his insight and patience. Long-continued and carefully controlled observations and experiments with generations of plants have led him to conclusions which have given the Evolution Theory a fresh start. His "Mutation Theory" is certainly one of the greatest advances since Darwin's day.

The General Idea.—The origin of species and varieties is an object for experimental inquiry. "Comparative studies have contributed all the evidence hitherto adduced for the support of the Darwinian theory of descent, and given us some general ideas about the main lines of the pedigree of the vegetable kingdom, but the way in which one species originates from another has not been adequately explained. *The current belief assumes that species are slowly changed into new types. In contradiction to this conception the theory of mutation assumes that new species and varieties are produced from existing forms by sudden leaps. The parent-type itself remains unchanged throughout this process, and may repeatedly give birth to new forms. These may arise simultaneously and in groups, or separately at more or less widely distant periods.* . . . . My work claims to be in full accord with the principles laid down by Darwin, and to give a thorough and sharp analysis of some of the ideas of variability, inheritance, selection, and mutation, which were necessarily vague at his time" (From preface to *Species and Varieties, their Origin by Mutation*" Chicago and London, 1905).

A Theoretical Implication.—De Vries's Mutation Theory involves the theoretical conception that "the characters of the organism are made up of elements that are sharply separated from each other. These elements can be combined in groups, and in related species the same combinations of elements recur. Transitional forms like those that are so common in the external

features of animals and plants do not exist between the elements themselves, any more than they do between the elements of the chemist."

The Case of the Evening Primrose.—In 1886, De Vries began hunting about around Amsterdam for a plant which would show hints of being in what we may call a changeful mood. He tried over a hundred species, bringing them under cultivation, but almost all were disappointingly conservative. It seemed as if most of the species around Amsterdam were in a non-mutable state. It is possible, as Weismann suggested in one of his first evolutionary essays (1872), that in the life of species periods of constancy alternate with periods of changefulness. The human historian has often made a similar remark.

In the course of his wanderings around Amsterdam, De Vries came across a deserted potato-field at Hilversum—a field of treasure for him. For there he found his long-looked-for mutable plant, an evening primrose (*Œnothera lamarckiana*). Like its nearest relatives, *Œnothera biennis* and *Œnothera muricata*, which it excels in size and beauty of flowers, it probably came from America, where it is a native. It had probably "escaped" at Hilversum about 1875, and in the following ten years it had spread in hundreds over the field. It had been extremely prolific in its freedom, but that was not its chief interest.

Its chief interest was its changefulness. It had, so to speak, frolicked in its freedom. Almost all its organs were varying—as if swayed by a restless tide of life. It showed minute fluctuations from generation to generation; it showed extraordinary freaks like fasciation and pitcher-forming; it showed hesitancy as to how long it meant to live, for while the majority were biennial, many were annual, and a few were triennial; it showed what can hardly be otherwise described than as new species in the making.

It is possible that the prolific multiplication in a new environment may have had something to do with the awakening of the impulsive mutability.

In 1887, a year after his discovery of the potato-field, De Vries found two well-defined new forms—a short-styled *O. brevistylis* and a beautiful smooth-leaved *O. lævifolia*—distinguishable from the parent *O. lamarckiana* in many details. He hailed these as two new "elementary species," * and he applied one of the crucial tests of specific or subspecific rank: Did they breed true? He found that this was so; from their self-fertilised seeds similar forms arose. Neither of the two new forms was represented in the herbaria at Leyden, Paris, or Kew; neither had been described in the literature of Onagraceæ. They seemed to be distinctively new. It is interesting to note that in 1887 there were few examples of these two new elementary species, and that each occurred on a single plot in the field. The impression conveyed was that each had arisen—by a sudden mutation—from the seed of an individual parent.

The next chapter in the famous investigation began with a transference of samples of the new forms and the parent stock—partly as plants and partly as seeds—from the potato-field at Hilversum to the botanic garden at Amsterdam.

The three stocks gave rise under cultivation to many thousands of individuals, which bred true along certain lines, and yet gave rise to other new forms. In short, De Vries had found a plant in process of evolution. The predisposition to mutability—which remains a mystery—was present, De Vries gave it scope, and like the primeval gardener he had the pleasure of giving names to a crop of new creations which emerged before him. From each of his three samples there arose several distinctive groups—which if they had been found in nature would have been reckoned as distinct species of evening primrose. But the most interesting feature was the apparent abruptness in the origin of the new

* By an "elementary species" is meant simply a group of individuals which agree with one another and differ from other groups in a certain number of characters, normally constant through successive generations.

forms. They seemed to arise by leaps and bounds, by organic jerks; they illustrated what De Vries has called "Mutation."

Besides the smooth-leaved *O. lævifolia* and the short-styled *O. brevistylis*, both of which appeared in the potato-field, the cultivation of *O. lamarckiana* resulted in the emergence of seven constant elementary species—*O. gigas* (rare), *O. rubrinervis*, *O. oblongata*, *O. albida*, *O. leptocarpa*, *O. lata*, and a dwarf *O. nanella*. Besides these there were a few inconstant variants and a few which were sterile.

One form, *O. scintillans*, that only appeared eight times, was not constant like the others. When self-fertilised it produced *O. oblongata*, *O. lamarckiana*, and others like itself.

It is interesting to notice that some of the forms—*e.g.* *O. oblongata*—were produced over and over again; that five of the new forms appeared afterwards in the field or from seeds collected in the field, which shows that the cause of their origin was not to be found in the cultivation.

As De Vries says, the new elementary species arise suddenly without transitional links; for the most part they are quite constant; within the limits of their essential constancy they exhibit similar minor fluctuations; they are usually represented by numerous individuals within the same period of time; the observed changes affect many organs and parts, and in no definite direction; and the mutability seems to be periodic, not continuous.

If cases like that of *O. lamarckiana* are indicative of what often occurs and has occurred in nature, then our view of the evolution-process must be in several respects modified.

It will be necessary to distinguish more sharply between fluctuating variations and discontinuous mutations. If a new elementary species may arise as it were ready-made, "at a single advance," it is not necessary to hold to the formula that species have arisen by the gradual accumulation (under selection) of minute individual variations. As mutations occur in large numbers and occur repeatedly and are very constant, the familiar difficulties in regard to the swamping of novelties, the inappreciable value of incipient stages, the apparent non-utilitarian character of some specific differences, and so on, will be greatly

lessened. The reader may be referred to Prof. T. H. Morgan's *Evolution and Adaptation* (1903) for a valuable discussion of the advantages of the Mutation Theory.

De Vries's Analysis of Variation.—In order to appreciate more thoroughly the importance of the changes which De Vries has necessitated in our evolutionary conceptions, we must briefly refer to his analysis of the distinct phenomena which have been too often unfortunately slumped under the title "Variations."

"Elementary Species."—In many groups of organisms which are usually called Linnæan species, there are several or numerous "subspecies," or "varieties." They remain more or less constant in their characters from generation to generation, they breed true in artificial conditions, they are not local races with similar modifications; De Vries calls them "elementary species." Thus there are about two hundred "elementary species" of the common Crucifer, *Draba verna*, and a few "elementary species" of the common European heartsease (*Viola tricolor*), and so on.

"The systematic species," De Vries says, "are the practical units of the systematists and florists, and all friends of wild nature should do their utmost to preserve them as Linnæus has proposed them. These units, however, are not really existing entities; they have as little claim to be regarded as such as the genera and families have. The real units are the elementary species; their limits often apparently overlap, and can only in rare cases be determined on the sole ground of field-observations. Pedigree-culture is the method required, and any form which remains constant and distinct from its allies in the garden is to be considered as an elementary species" (1905, p. 12).

Elementary species are considered to have originated from their parent form in a progressive way; they have succeeded in attaining something quite new for themselves.

Retrograde Varieties.—De Vries applies this term to those numerous forms which have thrown off some peculiarity characteristic of their ancestors. Like elementary species they may arise

suddenly, but while "progressive steps are the marks of elementary species, retrograde varieties are distinguished by apparent losses." Retrograde varieties usually differ from their parent species by a single sharp character only,—they have lost pigment, or hairs, or spines, and so on; while elementary species are distinguished from their nearest allies in almost all organs. Moreover, the same kind of retrograde variety occurs repeatedly in different series of species, hence the long lists of unrelated varieties called by the same varietal title—*e.g. alba, inermis, canescens*, or *glabra*.

"Varieties differ from elementary species in that they do not possess anything really new. They originate for the greater part in a negative way, by the apparent loss of some quality, and rarely in a positive manner by acquiring a character already seen in allied species" (1905, p. 152).

Ever-sporting Varieties.—De Vries uses this term to describe cases like the striped larkspur, which for centuries has gone on producing unstriped as well as striped flowers. "Its changes are limited to a rather narrow circle, and this circle is as constant as the peculiarities of any other constant species or variety. But within this circle it is always changing, from small stripes to broad streaks, and from them to pure colours. Here the variability is a thing of absolute constancy, while the constancy consists in eternal changes!" Plants with variegated leaves, with double flowers, with fasciated branches, with peloric flowers, and so on, often illustrate the "ever-sporting" tendency. The common snapdragon (*Antirrhinum majus*) is a very good case,—the striped variety, for instance, cannot be fixed. There is some inherent instability in the combination of unit-characters in these ever-sporting varieties.

Fluctuations.—De Vries applies this term to the continually occurring individual variations. "It is normal for organisms to fluctuate to and fro, oscillating around an average type. Fluctuations are linear, amplifying or lessening the existing

qualities, but not really changing their nature. They are not observed to produce anything quite new; they always oscillate around an average, and if removed from this for a time, they show a tendency to return to it." They are inadequate ever to make a single step along the great lines of evolution, whether progressively or retrogressively. They do not form the raw material of evolution, as has often been supposed. But, we submit, it is difficult with our present knowledge to discriminate between a fairly large fluctuation and a small mutation.

Mutations.—"In contrast to the ever-recurring variability, never absent in any large group of individuals, and determining the differences which are always to be seen between parents and their children, or between the children themselves, we have to rank the so-called sports or single varieties, not rarely denominated spontaneous variations, for which I propose to use the term 'mutations.' They are of very rare occurrence, and are to be considered as sudden and definite steps" (1905, pp. 190–1).

"De Vries recalls Galton's apt comparison between variability and a polyhedron which can roll from one face to another. When it comes to rest on any particular face, it is in stable equilibrium Small vibrations or disturbances may make it oscillate, but it returns always to the same face. These oscillations are like the fluctuating variations. A greater disturbance may cause the polyhedron to roll over on to a new face, where it comes to rest again, only showing the ever-present fluctuations around its new centre. The new position corresponds to a mutation" (T. H. Morgan, 1903, p. 289).

According to De Vries, mutations have furnished the material for the process of evolution.

The Oldest Known Mutation.—A few years before the close of the sixteenth century (1590), Sprenger, an apothecary of Heidelberg, found in his garden a peculiar form of *Chelidonium majus* or greater celandine. It was marked by having its leaves cut into narrow lobes with almost linear tips, and by having the

petals also cut up. This sharply defined new form suddenly appeared among the plants of *Chelidonium majus* which the apothecary had cultivated for many years. It was recognised by botanists as something quite new, and eventually it got the name *Chelidonium laciniatum*; it was not to be found wild, or anywhere except in the Heidelberg garden. But from the first this new cut-leaved celandine proved constant from seed. It has been naturalised in England and other countries, and is sometimes now found as an "escape." Its origin by mutation seems as certain as its constancy. It is further of interest to note that in crosses with *C. majus* it follows the law of Mendel.

Summary.—De Vries has done great service in analysing the complex concept of variation; in sharply contrasting individual fluctuations and mutations; in defining "elementary species," "retrograde varieties," and "ever-sporting varieties"; in observing the actual origin by mutation of stable new varieties or subspecies of *Œnothera lamarckiana* and some other plants; in showing by historical research combined with experiment that many stable stocks of cultivated plants have arisen by mutation; and by corroborating throughout the fundamental idea that "the characters of organisms are composed of units sharply distinguished from one another."

The contrast between fluctuations and mutations is so important that we may state it once more. (1) Fluctuations are continually occurring generation after generation: mutations are rare and occur intermittently. (2) Fluctuations give rise to a series of minute differences which may be arranged on a frequency curve, according to the laws of chance: mutations may be large or small, and their occurrences do not illustrate any ascertained law of frequency. (3) Fluctuations do not lead to a permanent change in the mean of the species unless there be very rigorous selection, and even then, if the selection be slackened, there is regression to the old mean: mutations lead *per saltum* to a new specific position, and there is no regression to the old mean.

(4) Fluctuations do not yield anything really new, they imply a little more or a little less of characters already present: mutations are novelties, they imply some new pattern, some new position of organic equilibrium. According to De Vries's theory, no new species can be established without mutation. "When a mutation has occurred a new species is already in existence, and will remain in existence, unless all the progeny of the mutation are destroyed." . . . The phrase "survival of the fittest," as describing a process of evolution, ought to be replaced by "survival of the fittest species." According to De Vries, species originate by mutation instead of by the continuous selection of fluctuations. "Natural Selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest."

In regard to these far-reaching conclusions it should be noted that while De Vries has given much convincing evidence in regard to plants, we have as yet very slight evidence of the origin of species of animals by mutation. We know of many discontinuous variations among animals, but the subsequent history of these is not known except in a few cases. It must be remembered that, morphologically regarded, the whole vegetable kingdom does not correspond to more than the first three or four phyla in the animal kingdom—to the Protozoa, Porifera, and Cœlentera, where, as in plants, the contrast between germ-plasm and somatoplasm has not been accentuated, as it is in higher animals. It is quite conceivable that a mode of evolution common among plants may be rare among animals. It is difficult at present to apply the mutation concept with security to the animal kingdom.

The idea of mutation is very welcome because it lessens the burden which it has been found theoretically necessary to lay on the shoulders of the selection hypothesis, and because it fits in well with the *a priori* convictions which some naturalists have as to the autonomy of the organism, that it is as much a self-changing insurgent Proteus as a pawn in a game which the Environment plays. But because it is so welcome, it is to be entertained

Fig. 22.—Mutations of Hart's Tongue Fern (*Scolopendrium vulgare*). After Lowe.

1, Typical; 2, variety sagittato-cristatum; 3, reniforme; 4, cristatum; 5, contractum; 6, stansfieldii.

[*Facing p.* 98

the more cautiously. An authority on domesticated animals, Prof. Keller of Zürich, finds but little evidence of it in the history of the well-known stocks.

It seems to us that in emphasising the importance of mutations De Vries has swung to the extreme of greatly depreciating the importance of fluctuations. Until we know more about animal mutations, it does not seem to us legitimate to deny that fluctuations may form, as Darwin believed, an important part of the raw material on which selection operates.

We cannot but regard with suspicion the distinction between large fluctuations and small mutations. It seems to us a verbal distinction.

Finally, it must be remembered that, as De Vries frankly points out, we are ignorant in regard to the conditions in which mutations occur. The Mutation Theory does not as yet give us a theory of mutations.

" *Pure Lines.*"—The position held by De Vries has been strengthened by the work of Johannsen and Jennings on " pure lines." If we succeed in starting a " pure line "—" the progeny of a single self-fertilised homozygous plant"—say an innately exceptional bean-plant with very large seeds, we shall find slight individual differences in the size of the beans from generation to generation ; if we take the biggest and the smallest of these and start afresh, we find that their progeny are neither larger nor smaller than the average. The original bigness was a fixed mutation ; the other differences were probably mere modifications and non-transmissible. If we take a considerable number of the largest beans and the smallest beans from a field and sow them, we are likely to get in the progeny of the former a larger average size than in the progeny of the latter, for we are almost sure to have started with a number of beans which are innately (not modificationally) large-sized and small-sized. What Johannsen did for the bean and some other plants, Jennings has done for the slipper-animalcule, *Paramœcium.* He isolated eight pure lines differing in average size, and found that he made no progress by selecting the largest in an established large pure line, the exceptional largeness being probably the accidental result of peculiar nurture. Selection from a mixed population, however, resulted, as in the case of the beans, in a distinctly altered average size.

The experiments were made with consummate carefulness, but it is difficult to accept the idea of the rigid fixity of the hereditary characters in a pure line. It may be that in some cases, such as beans, the viable limit of size has been reached. It may also be that the variational steps that count do not occur often. Perhaps some time must elapse before the organism takes another step.

Prof. Castle asks: "Is it not possible that along with the striking size differences due to nutrition there may occur also slight size differences due to germinal variation within the pure line, that is owing to variations in the potency of the same unit-character or combination of unit-characters?" And he points to Woltereck's successful selecting-out of a variation in a parthenogenetic pure line of the water-flea, *Hyalodaphnia*. He selected forms which showed the exceptional occurrence of a rudimentary eye, and definitely increased the degree of development of that organ and the frequency of its occurrence (up to 90 per cent.).

In short, it is premature to abandon belief in the efficacy of selection even in pure lines.

§ 8. *Causes of Variation*

In regard to the causes of variation it is too soon to speak, except in tentative whispers. What Darwin said must still be said: "Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied."

Variability.—The difficulty which every naturalist has felt in trying to define the concepts of variability and variation is due to the fact that living creatures are individualities—in some degree, personalities. In the ocean of matter and energy organisms are, as it were, whirlpools, each one with a particular character of its own. They are animate systems, each with a unity or individuality which we cannot fully interpret. They have the power—again an ultimate prerogative—of giving rise to other whirlpools, to other animate systems, which tend to be like themselves. But because each organism is a very complex whirlpool in a very complex environment, and because a living individuality cannot reproduce others without subtle molecular manœuvres which we

know only in a far-off sort of way, one individuality is very unlikely to reproduce an absolute facsimile of itself. It is of the very essence of a living thing to change, and an individuality cannot be halved. From this point of view, variation is a primarily normal occurrence, and breeding true has secondarily come about as the result of restriction. In short, variability is a primeval character of organisms. We cannot explain variability; it is a datum in the world of life. We may, however, try to show in certain cases how it operates and what conditions help or hinder it.

The unending problem of life is to establish some sort of *modus vivendi* between an extremely complex and changeful animate system and the extremely complex and changeful environment in which it lives and moves and has its being. In all viable organisms this equilibration has been established, and it is plain that those organisms which could secure an entailment of this equilibration would be the organisms to survive. The producers of survivable descendants survive in them—an obvious economy of successful experiment, if such a point of view can be entertained.

We have seen that during the early stages of development there is often a visible segregation of a lineage of germ-cells which do not share in body-making, but continue like the fertilised ovum. This distinction between somatic cells which undergo differentiation and germ-cells which retain the heritable qualities intact is obviously an advantageous method of entailing on successive generations that valuable asset which we have called organic equilibration. It also economises and facilitates the process of reproduction.

But in spite of this almost universal device, the general tendency of which is to secure persistence, continuity, and complete hereditary resemblance, there is abundant opportunity left for the assertion of that variability which we believe to be a primary quality of vital units. Thus an inquiry into the causes of variation seems to us to be in the main an inquiry into the opportunities for the reassertion of a pristine tendency which the

continuity of the germ-plasm has to some extent restricted. The stream of life passing through a continuous lineage of germ-cells is, so to speak, hemmed in, but it continually tends to deviate from this course, and there are not a few opportunities—some normally recurrent, some more accidental—which allow of this or even prompt it. In some cases, as we have said, it is impossible to distinguish offspring from parent, or brother from brother, or cousin from cousin. On what does this completeness of hereditary resemblance (*i.e.* the absence of variation) depend ?

It means, in the case of unicellular organisms, that the separated parts are identical in substance and carry on the complete organisation of the parent cell in absolute integrity. In the case of multicellular organisms it depends on the same thing. The cell which in the embryo begins the germ-cell lineage may be identical with the fertilised ovum, and the complete heritage may be continued intact through successive cell-divisions until the next generation is started, and the process begins anew. The completeness of hereditary resemblances depends, in Bateson's phrase, on " that qualitative symmetry characteristic of all non-differentiating cell-divisions."

It seems, therefore, useful to say that variation is " the expression of a qualitative asymmetry beginning in gametogenesis. Variation is a novel cell-division." But to tell what specific cause induces this novelty is still beyond our power. Yet we can point to certain conditions which may induce novelty or qualitative asymmetry in gametogenesis. Thus, there is the complex changeful environment of the developing germ-cells, there is the possible struggle of analogous hereditary units or determinants for sustenance, there is the complex process of reduction which occurs during the maturation of the germ-cells, and there are the chances of new combinations and permutations in fertilisation.

Results of Amphimixis.—That amphimixis is one of the provocatives of variations is strongly suggested by what results when two breeds

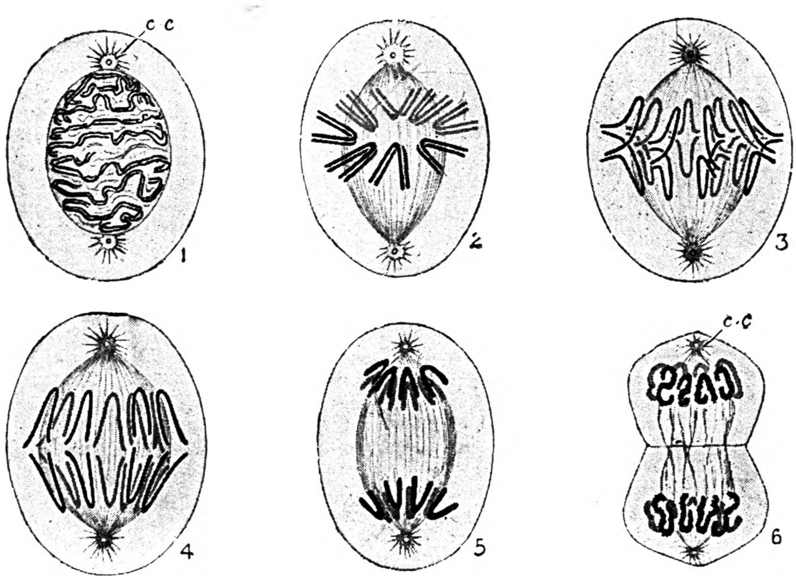

FIG. 23.—Karyokinesis. (After Flemming.)

1, Coil stage of nucleus; *cc* centrosome; 2, Division of chromatin into U-shaped loops, and longitudinal splitting of these (astroid stage); 3, 4, Recession of chromosomes from the equator of the cell (diastroid); 5, nuclear spindle with chromosomes at each pole, and achromatin threads between; 6, Division of the cell completed.

[*Facing p.* 102.

are interbred. As Prof. Cossar Ewart says *: "Domestic animals reproduce themselves with great uniformity if kept apart; but the moment one mixed up two different races, strains, or breeds, one did something that was difficult to put in words, but the result was what has been best described as an 'epidemic' of variations."

On the other hand, Hatschek and others have pointed out that amphimixis acts as a check on variability, obviating heterogeneous idiosyncrasies. This was suggested even by Lamarck: "In reproductive unions the crossings between the individuals which have different qualities or forms are necessarily opposed to the continuous propagation of these qualities and these forms." Similarly Darwin said: "When species are rendered highly variable by changed conditions of life, the free intercrossing of the varying individuals tends to keep each form fitted for its proper place in nature."

Combinations of Chromosomes.—Prof. H. E. Ziegler has given much attention to the number of possible combinations of parental chromosomes in the offspring, supposing the distribution to be fortuitous. If the normal number of chromosomes in a species is n, the number of tetrad groups is $\frac{n}{2}$, the number of possible combinations in the mature germ-cells is $\frac{n}{2} + 1$, and the number of possible combinations in the fertilised egg-cell is $\left(\frac{n}{2} + 1\right)^2 = \frac{n^2}{4} + n + 1$.

If the normal number of chromosomes be 8 (as in the fluke often found parasitic in frogs, *Polystomum integerrimum*), the number of tetrad groups is 4, the number of possible combinations in the mature germ-cells is 5, and the number of theoretically different offspring is 25, *i.e.* on the assumption that the chromosomes are heterogeneous. But according to the laws of chance certain combinations are much more frequent than others; the larger the number of tetrad groups the more frequent is the occurrence of an approximately equal number of paternal and maternal chromosomes in the germ-cell.

Sutton puts the matter as follows. An individual receives from his father 4 chromosomes, A, B, C, D, and from his mother (an equal number) a, b, c, d. The immature germ-cell has A, B, C, D; a, b, c, d. These group themselves in four tetrads, each composed of two double chromosomes, two maternal and two paternal, Aa, Bb, Cc, Dd. The mature germ-cell receives one chromosome from each

* Discussion on Heredity in Disease, *Scottish Med. and Surg. Journal*, vi 1900, p. 308.

tetrad, and there are 16 possible combinations—viz. a, B, C, D; A, b, C, D; A, B, c, D; A, B, C, d; a, b, C, D; a, B, c, D; a, B, C, d; a, b, c, d; and eight others which may be got by replacing small letters by capital letters and *vice versâ*. The number of possibly different offspring would be 16^2.

Sutton gives the following table, which is of some interest as suggesting the possibilities of variation.

Normal number of chromosomes	Number of Tetrad-groups	Number of combinations in the mature germ-cells	Number of possibilities in the offspring
8	4	16	256
12	6	64	4,096
16	8	256	65,536
24	12	4096	16,777,216

Summary.—In certain moods biologists are accustomed to say that they do not know anything in regard to the causes of variation. They imply that it is of the essence of living creatures to vary, that variability is a primary property of organisms. The sequence of generations is a life stream, changing as it flows.

In other moods, however, biologists often point out how natural it is that organisms should vary. When the body of the parent is a-making, a lineage of germ-cells is started and the unspecialised descendants of these develop into offspring, which are on the whole like the parent because they are made of the same stuff. "True" twins developed from one ovum are usually almost facsimiles of one another. Why should not the offspring be a facsimile of the parent? Sometimes, *to our eyes*, it is quite confusable with the parent, but this is not common. Why not?

1. It is common to point out that the germ-cell which is liberated to become an offspring is not likely to be identical with the germ-cell which developed into the parent. It has been sojourning in the parent's body, exposed to a variable food stream and often to a variable complex environment, partly somatic and partly external. Is it likely to be exactly the same as the original germ-cell from which it is descended by continuous cell-division?

The experiments of Prof. W. L. Tower, in particular, suggest that important external changes may provoke changes in the germ-cells without necessarily affecting the parental body. He subjected full-grown potato-beetles (*Leptinotarsa*) to peculiar conditions of temperature and humidity during the time when the eggs were maturing, and found that "mutations" occurred in a certain proportion of the offspring. The parents were not affected, having passed the plastic stage; and some of the eggs were not affected at all. Moreover, the same environmental peculiarity did not always produce the same mutation in the offspring. But what Tower's experiments forcibly suggest is this: that deeply saturating environmental changes may serve to pull the trigger of germinal variability.

2. It is also to be remembered that if the chromosomes stand in some definite causal relation to heritable qualities, as seems practically certain, then the maturation reduction of the chromosomes to one half their original number offers an opportunity for variation.

3. It is likely that fertilisation or amphimixis—the intimate and orderly union of two sets of hereditary contributions which have often had very different histories—will promote variation. It is difficult to believe that it does not bring about new permutations and combinations.

4. It is possible that variations may also arise in a less conceivable fashion—"bathmically," as the phrase goes—for unknown internal reasons. It is not absurd to suppose that the germ-plasm grows from generation to generation, and, in growing, changes—because it is its nature so to do.

Apart from variation of internal origin and positive modification of external origin, we must remember that the offspring may differ from its parents through non-expression of certain items of its inheritance, the non-expression being due to the absence of the appropriate liberating stimulus. This kind of deviation may of course be obliterated next generation, when the full environment allows the latent character to re-express itself.

CHAPTER IV

COMMON MODES OF INHERITANCE

"Lord, I find the genealogy of my Saviour strangely checkered with four remarkable changes in four immediate generations.

1. Roboam begat Abia; that is, a bad father begat a bad son.
2. Abia begat Asa; that is, a bad father a good son.
3. Asa begat Josaphat; that is, a good father a good son.
4. Josaphat begat Joram; that is, a good father a bad son.

I see, Lord, from hence, that my father's piety cannot be entailed; that is bad news for me. But I see also, that actual impiety is not always hereditary; that is good news for my son."—THOMAS FULLER, *Scripture Observations*, No. viii.

§ 1. *Though Prediction in Individual Cases is insecure, there are some Common Modes of Inheritance.*
§ 2. *Certain Necessary Saving Clauses.*
§ 3. *Blended Inheritance.*
§ 4. *Exclusive Inheritance (Unilateral, Absolutely Prepotent, or Preponderant).*
§ 5. *Particulate Inheritance.*
§ 6. *Alternative Inheritance.*
§ 7. *Summary of Possibilities.*

ESPECIALLY among the lower animals, the offspring sometimes appear to us as if they were perfect reproductions of the parents, and we venture to speak of complete hereditary resemblance. Thus, in a crowd of Myriapods collected from one place at the same time, no individual peculiarities could be detected. A daughter-Hydra may be easily obtained which seems identical with the parent. A series of generations of green-flies or Aphides may be studied and no individual peculiarities discovered.

In other words, there seem to be cases in which generation succeeds generation without any variation.

But there is every reason to suspect that in most cases the apparent absence of variation is illusory, and due to a lack of sufficiently intimate acquaintance with the individual organisms. The sheep which seem "all the same" to the careless eye are often known individually by the shepherd, and it is easy to demonstrate that the peas in one pod are often far from being alike. Similarly, the members of a group of individuals may seem "all the same" even to the naturalist's eye, but minute differences are soon detected by the expert who has devoted years to becoming intimately acquainted with that particular type. There are observable differences between sister-bees or ants, between the rooks from one clutch or the pigs from one litter. Even when there is only one parent—*e.g.* a self-fertilising liver-fluke or a parthenogenetic water-flea—there may be variations among the descendants. There is no doubt, however, that the range of variability differs greatly in different types, and it is obviously in cases where individual peculiarities are frequent and well marked that we can most hopefully study the relations of resemblance and difference between parents and offspring, or between the members of a series of generations. In horses and dogs, in sheep and cattle, in rats and mice, in rabbits and guinea-pigs, in pigeons and fowls, in butterflies and small, rapidly breeding crustaceans, in wheat and barley and maize, in peas and stocks, and in man himself, there is ample opportunity for studying *the modes of inheritance.*

§ 1. *Though Prediction in Individual Cases is insecure, there are some Common Modes of Inheritance*

When we are dealing with the generations of an animal or plant in regard to which previous observation has shown us that the members of the species are strikingly uniform in their characters, we may venture with some security to predict that

the offspring of a pair will as usual exhibit more or less complete hereditary resemblance to their parents and ancestors. And yet this prediction may be falsified, for variations may suddenly crop up without known cause.

Similarly, when we are dealing with the generations of a so-called "pure-bred" race of animals or plants, we may venture with some security to predict that the offspring of a pair will exhibit, as regards their more essential features, a large measure of complete hereditary resemblance to their parents and ancestors. And yet in individual cases this prediction also may be falsified; for no known reason a "freak" or "sport" may unexpectedly appear.

When we consider the variable nutritive conditions of the germ-cells, the subtle processes of maturation and fertilisation, and the intricate nature of the environment appropriate to each development, we cannot be surprised that the result may often belie individual prediction. The possibly anecdotal instance, cited by Lucas, of the twin children of an Antillean negress—one white with long hair, the other black with woolly hair—may serve as a diagrammatic illustration.

On the other hand, experience shows that, in spite of uncertainty in regard to individual cases, there is often perfect certainty as to the average results where we have to do with large numbers; that the degree of resemblance to parents and ancestors is sometimes capable of precise prediction; that in particular sets of cases (Mendelian phenomena, see Chapter X.) we can definitely predict how many of the offspring will be like the parents, how mary like one grandparent, how many like another; and that, apart from such statistical generalisations, there are what we may call *alternatives of expectation* with varying degrees of probability. In other words, *there are certain more or less well-defined modes of hereditary resemblance which occur very frequently,*

§ 2. *Certain Necessary Saving Clauses*

A discussion of the different modes of hereditary resemblance is somewhat hampered by an exuberant terminology, and by the fact that different authors have sometimes used the same term in different ways. We read of inheritance being unilateral and bilateral, unisexual and bisexual, blended and conspired, neutralised and combined, direct and collateral, atavistic and progressive, reversionary, exclusive, particulate, alternative, Mendelian, and so on. With the progress of investigation the redundant terminology is being pruned. Thus, many modes of inheritance which seemed at first discrepant are now recognised to fall within Mendelian formulation.

We have seen that cases of apparently very complete hereditary resemblance may be illusions due to our inability to appreciate the differences that really exist ; but on the other hand, we must guard against the error of supposing that the frequently conspicuous differences between offspring and their parents necessarily mean an incompleteness in the inheritance itself. The fact that the resemblance often reappears in the third generation shows that the incompleteness is often *not in the inheritance*, but simply in its *expression*. The characters were probably there *in posse* in the germinal matter, but they were neutralised, kept latent, silenced—we can only use metaphors—by other characters, or else they never met with the stimulus necessary for their expression in development. We can imagine the son of a lavish millionaire reacting to plain living, the superficial inference that the money had been lost, and the contradiction of this in the third generation.

Similarly, when a male offspring is compared with the mother, a female offspring with the father, it is important to bear in mind that the difference in sex may account for some of the apparent differences in detailed characters. Through functional correlation, the differentiation of sex may bring about the non-

expression or the modified expression of a peculiarity which was none the less transmitted in its entirety, as the third generation may demonstrate.

Another fact that must be borne in mind is the difficulty of distinguishing even with probability between hereditary and acquired resemblances. The Alpine plants which Nägeli transplanted to a southern garden were changed by their new surroundings; their descendants were likewise changed, and the new characters reappeared with constancy generation after generation. But this was acquired or modificational, not hereditary or innate resemblance, as was shown by the fact that removal from the garden to poor gravelly soil was followed by a reappearance of the original Alpine characteristics. Some interesting cases have been alleged where the reappearance of the Alpine characters was not immediate, but *gradual*. We require, however, more circumstantial details in regard to these cases.

§ 3. *Blended Inheritance*

In this mode the special characters of the two parents are intimately mingled in the offspring. The colour of the hair may be an almost precise average between that of the blonde mother and that of the black-haired father. In repose the boy's face may seem markedly paternal; it is moved with emotion, and he is his mother's image. This blending is particularly well seen in some plant hybrids, where the offspring shows in leaf-venation, in size of epidermic cells, in number of stomata, in length of style, in degree of hairiness, and so on, what seems like an accurate mean of the two parents. Prof. J. M. Macfarlane has given some beautifully precise data regarding the blending of characters in plant hybrids.

When in any given character of the offspring we can detect both maternal and paternal peculiarities, we call the inheritance

blended; but there may be quantitatively more of the maternal quality or of the paternal quality expressed, and then we say

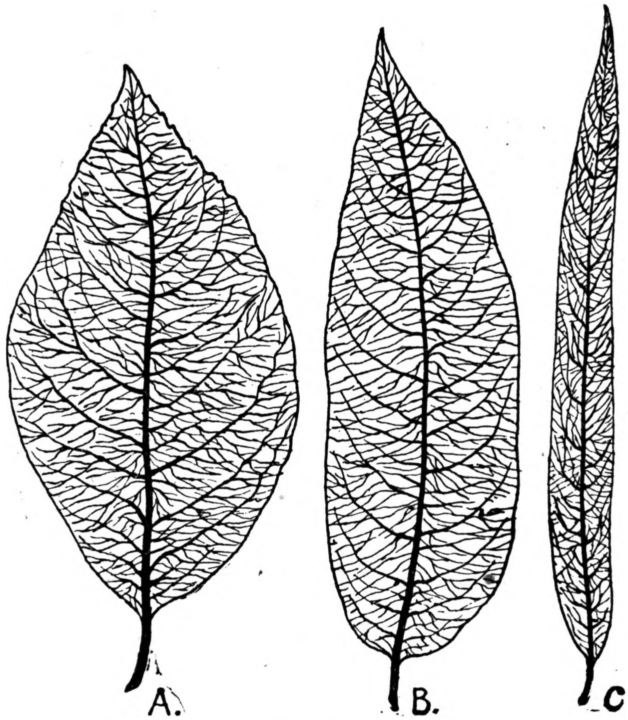

FIG. 24.—Leaves of Willow: A, of one parent; C, of the other parent; B, of the hybrid intermediate between them. (After Wiesner.)

that in the blended inheritance or in its expression one of the two parents is *prepotent*. An increase in the predominance of the characteristics of one parent leads to the second common mode of inheritance, which we call *exclusive*.

W. E. Castle (*Journ. Washington Acad. Sci.*, VII., 1917, 369–87) states his conclusion that "aside from colour, there are very few valued economic characters in our domestic animals which are not inherited after the manner of blending." It must be noted, however, that in a very large number of cases of indubitable Mendelian inheritance the hybrid offspring is intermediate between the two parents. What is called "incomplete dominance" may simulate true blending, such as is probably illustrated in human stature.

§ 4. *Exclusive Inheritance (Unilateral, Absolutely Prepotent, or Preponderant)*

When in the expression of the biparental inheritance there is, as regards a given character, an absolute prepotency on one side or the other, or, conversely, an apparent reduction of the maternal or paternal peculiarities to zero, the inheritance is called *exclusive.* The terms "unilateral," "absolutely prepotent," or "preponderant" are also used. This mode of inheritance is oftenest seen in regard to particular characters, but it is sometimes consistently illustrated in so many parts of the organism that observers say of the whole offspring that it favours its sire, or that it takes after its mother.

In reference to a few characters a general statement may sometimes be made with security to the effect that, on the average, the father is prepotent in certain respects and the mother in others. Thus, in regard to stature of human beings (in Britain), it seems certain that the father is usually prepotent; that is to say, on the average children attain to a stature which is nearer that of the father than that of the mother. But every statement of this sort must be based on carefully collected statistics, and not on the "impressions"—however strong—which breeders have often formulated as laws.

There are many popular generalisations which ascribe to each of the parents the power of transmitting particular characteristics. Thus, the father is supposed to have to do with external form, the mother with temperament and the organs of vegetative life. While particular statements in respect to this are interesting and should be accumulated in as large numbers as possible, almost all the generalisations, including the one instanced, are mere guesses. At present, we can only say that in some cases the expression of the inheritance as a whole, or in regard to particular characters, may resemble one parent more or less exclusively. In other words, the father sometimes seems absolutely

prepotent, the mother sometimes seems absolutely prepotent, but the characters in regard to which the prepotency is exhibited usually vary from case to case. Goethe may have been quite accurate in saying:

> Vom Vater hab' ich die Statur,
> Des Lebens ernstes Führen;
> Vom Mütterchen die Frohnatur
> Und Lust zu fabuliren.

But this cannot be generalised as a law of inheritance!

There seems to be a widespread belief among breeders that external form depends upon the father, while temperament and visceral organs depend upon the mother. But this does not stand examination. Nor can we rely with security on the opinion of many horse-breeders—*e.g.* Stephens—that the sire almost always counts for most all round; for it has to be remembered that a sire is mated with very few dams as good as himself. Buffon hazarded the conclusion that the mule resembles the father ass more than the mother mare, and the hinny resembles the father horse more than the mother ass; but he dealt only with superficialities. Crossings between humped zebu cattle and those without humps show that the hump is inherited in some degree, whether it was possessed by the ox or the cow; and the same is true in regard to camels with one or two humps, and in regard to crossings of wild boar and sow or *vice versâ*.

There is no doubt that what looks like well-marked "unilateral inheritance" is not infrequent, where the son is, as they say, the very image of his father, or the daughter the reflection of her mother; or, even more frequently, where the inheritance is, as they say, "crossed," the son taking after the mother, and the daughter after the father. But to generalise the latter into a formula, as some dog-breeders have done, "Chien de chienne, et chienne de chien," is quite illegitimate. The result will depend on which of the parents has the mysterious quality of "prepo-

tency" ; and it may be that the father is "prepotent" in regard to some of the characters and the mother in regard to others. A negro in Berlin had by a white woman seven daughters who were markedly mulatto, and four sons who were white ; the inheritance was "crossed," but other cases forbid us from making any generalisation.

It must be carefully kept in view that where the expression of the inheritance markedly follows one parent, it does not in the least follow that the corresponding contributions from the other parent have been lost. It may be that the latter will reappear in the next generation, having simply remained latent in the custody of the germ-cells. And again, there are cases on record where the young boy resembled the mother and the young girl the father ; but as they grew up, the likeness was reversed—*i.e.* resemblances formerly obscure became conspicuous. Such cases seem to warrant our insistence on the distinction between the inheritance and the expression of the inheritance.

It must be carefully borne in mind that what we describe as a case of exclusive inheritance may be the first step in Mendelian inheritance. When a parent with a dominant unit character mates with one having a corresponding unit character recessive the offspring all show the dominant character.

§ 5. *Particulate Inheritance*

In some cases it seems that, *as regards a given character*, the peculiarities of the two parents do not blend, but are separately expressed in different parts. The combination is, as it were, too coarse-grained to be called a mixture or a blend. This is termed *particulate* inheritance.

A familiar instance is a piebald foal—the progeny of a dark-coloured sire and a light-coloured mare. The paternal hair is seen in some parts, the maternal hair in other parts. "Eye-colour is generally exclusive, but we get one or two cases per thousand in man, in which either the two irises differ in colour,

or the one iris shows different patches of colour" (Pearson, 1900, p. 452). The case of an English sheep-dog with a paternal eye on the one side of its head and a maternal eye on the other is vivid enough.

When there is a marked difference in the pedigree, the vigour, the age—in short, in the constitution—of the two parents, the same mode of inheritance may be illustrated in a succession of offspring. Thus a fine sire, paired with a commonplace mate, may be prepotent birth after birth; or a young mother mated with a worn-out male may have it all her own way in regard to inheritance, as well as in much else. On the other hand, when there are no such marked differences between the parents, the inheritance may be a blend in one offspring, exclusive in another, particulate in a third. Moreover, in the same offspring, different sets of characters may illustrate different modes of inheritance. Thus we see that these modes of inheritance are merely useful descriptive terms, helping us to keep our facts in order, but not directly aiding us in their interpretation. They point to the need of some unifying conception, which shall enable us to understand how all these alternatives are possible.

In large families there is sometimes observable an interesting change in the direction of preponderance in the successive children. With a virile middle-aged father and a much younger mother, the older children may be markedly paternal in the expression of their inheritance, the younger children as markedly of the maternal type. The Benjamin is the mother's very image, and after the father's own heart.

Similarly, it has been observed that the first fertilised, almost immature ova of a rabbit, liberated by an ovulation subsequent to the first pairing, resulted in offspring which took after the male. If, on the other hand, the doe was served, not at the right time, but a week or ten days later, the young were all exactly like the mother.

Such cases suggest the conclusion that the expression of

inheritance follows the parent whose germ-cells are the riper at the time of fertilisation—an inference to which we shall return in discussing germinal selection.

The inference is further supported by Vernon's experiments in the hybridisation of sea-urchins, for he showed that the characters of the offspring incline to be those of the species whose gametes were relatively the more mature when fertilisation occurred.

§ 6. *Alternative Inheritance*

Since the re-discovery of Mendel's Law—to which we shall afterwards refer in detail—there has been a rapid accumulation of instances of what is called alternative or Mendelian inheritance, and some of the leading experimenters of to-day believe that this mode of inheritance will be found to include other modes like blended and particulate which seem at first sight distinct.

Let us follow one of these authorities, Dr. C. B. Davenport, in stating the fundamental ideas.

Experimental work has driven home the conception of unit-characters. That is to say, the characteristics of an organism may be analysed in some cases into distinct units that are inherited independently. About a dozen of these, for instance, have been *demonstrated* in the sweet-pea.

The theory, supported by experimental results, is that these unit-characters are represented in the germ-cells by what may be called representative particles, or primary constituents, or determiners, or factors, or genes, and that these cannot blend or compromise with other determiners of contrasted unit-characters. They are either there or not there. If two parents have the same unit-character (x) and the corresponding determiner or factor in all their germ-cells, all the offspring get a determiner x from both sides, and will have what is called a *duplex* or "double-dose" somatic expression of the character in question. When the germ-cells are formed in that offspring they will all have the determiner or factor x. If one parent has a unit-

character (x) which the other lacks, the offspring get a corresponding determiner x from one side only, and when the germ-cells are formed in that offspring half of them are supposed to have the determiner x and half not. This hypothetical process is called the segregation of determiners, and experimental results suggest its reality.

"The characteristic in the offspring that is due to a single (instead of the normal double) determiner is called a simplex characteristic. Such a characteristic is frequently distinguishable from one that is due to the double determiner by its imperfect development. Thus the offspring of a pure black-eyed and a blue-eyed parent will have brown eyes.

"It is a corollary of the foregoing that if the individual with a simplex character be mated to one lacking the character, half of the offspring will lack the determiner and half will be simplex, again, in respect to the character. If in both cases the character be simplex, the two like determiners will meet in one-fourth of the unions of egg and sperm, the two will both be absent in one-fourth of the unions, and one only will occur in half of the unions—such will be simplex again. If one parent have the characteristic simplex and the other duplex, then half of the offspring will have it simplex and half duplex.

"Starting with the principles just enunciated, we reach at once the most important generalisation of the modern science of heredity: "*When a determiner of a characteristic is absent from the germ-plasm of both parents* (*as proved* * *by its absence from their bodies*) *it will be absent in all of their offspring*" (*Eugenics*, 1910, pp. 8–9).

To illustrate the precision † with which the characteristics of offspring may be predicted in the best-studied cases, Davenport refers to eye-colour.

* Perhaps "inferred" would be a more accurate word than "proved." What is inherited in the germ-plasm is not necessarily *expressed* in development.

† See, however, Galloway (1912).

"Blue eyes are due to the absence of brown pigment. If there is a determiner for brown pigment in the germ-plasm, it will produce such pigment in the body that arises from that germ-plasm. The absence of iris pigment is proof of the absence of the pigment determiner from the germ-plasm. If both parents lack brown pigment, their offspring, being devoid of the determiner for brown pigment, will all lack brown pigment. As a matter of experience two parents with pure blue eyes will have only blue-eyed offspring."

The gist of Mendelism may be stated in two general propositions. (1) In the fertilised ovum there come together certain paternal and maternal factors or genes particularly associated with particular characters, but they do not mingle; on the contrary, in the history of the germ-cells of the offspring, there is a segregation of these genes, so that one member of each pair goes to one daughter-cell and the other to the other daughter-cell: they separate cleanly, without having influenced or contaminated one another except in rare cases. (2) In the segregation in question there is a free and independent assortment of the genes, so that the offspring of the first cross are in definite proportions as regards any particular character—some like the grandfather, some like the grandmother, and some like the parent.

If the two parents differ in having the qualities "colour" and "whiteness"—the fertilised ovum will include the factors of these—the hybrid offspring will be coloured, colour being *dominant* and whiteness *recessive*. But in the history, probably in the maturation, of the germ-cells of the offspring, the "colour" gene will be segregated in half of the germ-cells, and the "whiteness" gene in the other half. In the next generation, the offspring of the hybrids (bred together or with others of similar history), there will be on an average 25 per cent. with colour and pure as regards that, 25 per cent. with whiteness and pure as regards that, and 50 per cent. "impure dominants" like the parents, with the colour expressed (the dominant character), but with the whiteness latent (the recessive character).

CHAPTER V

REVERSION AND ALLIED PHENOMENA

" A man can never deny his ancestry."—LAWS OF MANU.
" Evolution ever climbing after some ideal good,
And Reversion ever dragging Evolution in the mud."—TENNYSON.

§ 1. *What is meant by Reversion.*
§ 2. *Suggested Definitions.*
§ 3. *Theoretical Implications.*
§ 4. *Phenomena sometimes confused with Reversion.*
§ 5. *" Skipping a Generation."*
§ 6. *Mendelian Interpretation of Reversion.*
§ 7. *Reversion in Crosses.*
§ 8. *Reversion of Retrogressive Varieties.*
§ 9. *Interpretations in Terms of Reversion.*
§ 10. *Further Examples of Reversion.*

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§ 1. *What is meant by Reversion*

MOST evolutionists—indeed, most naturalists—have ranked reversion as one of the facts of inheritance. Thus Darwin said (1881): " Any character of an ancient, generalised, or intermediate form may, and often does, reappear in its descendants after countless generations." Wallace, Spencer, Galton, and Weismann have all used the concept " reversion " as a convenient way of summing up a universally admitted series of cases, where organisms exhibit ancestral traits which their parents did not possess. As a *descriptive term* for summing up these cases, the word " reversion " is useful, convenient and, it

seems to us, entirely legitimate. When we go beyond the use of the word as a descriptive term, and use it as implying that the ancestral characters reappear because they are parts of the inheritance, which have been lying latent for generations, and have suddenly been allowed by some liberating stimulus to express themselves in development, we pass from fact to interpretation, from description to theory, and great care is necessary. For the fact that an organism exhibits some peculiarity characteristic of an ancestor does not necessarily imply that this is due to the rehabilitation of latent items in its inheritance.

Darwin believed that "an inherent tendency to reversion is evolved through some disturbance in the organisation caused by the act of crossing," and he gave such instances as the following. A goldfinch crossed with a plain yellow canary had offspring with stripes on the back and flanks. Darwin concluded that "this streaking must be derived from the original wild canary." He crossed a White Silkie hen with a black Spanish cock and got among the progeny a cock which looked like a rehabilitation of the original wild *Gallus bankiva* type. These facts have been confirmed, but it is now generally agreed that the Darwinian interpretation of them must give place to the Mendelian—that "in hybridising we restore the factor that is missing from one strain by introducing it from another strain; or we remove the added factor that veils the ancestral condition" (Davenport, 1910, p. 293, "The New Views about Reversion").

Illustrations.—A recognition of reversionary or atavistic phenomena is ancient. Plutarch gives the case of a Greek married woman who, having given birth to a black child, was brought to justice as an adulteress, and had science enough to allege in her defence that she was descended from an Ethiopian four generations back. This is paralleled by a case reported by De Quatrefages of two Virginian slaves, to whom a perfectly white child was born. "En voyant la couleur de son enfant, elle fut saisie de terreur, . . . mais son mari la rassura, en lui déclarant que son propre frère était blanc."

We do not mean that the instances just mentioned should be

taken as serious pieces of evidence in favour of the reversion *theory*, but they may serve to hint at the readiness with which the hypothesis of characters lying latent has been adopted. As we shall see, reversions in the strict sense are apparently few and far between.

A foal is sometimes born with a few stripes on its fore-legs, as if reminding us of striped wild horses. A dovecot with carefully bred pigeons was left to itself for some years, after which it was found to contain numerous blue pigeons, resembling in many ways the wild rock-dove (*Columba livia*). A

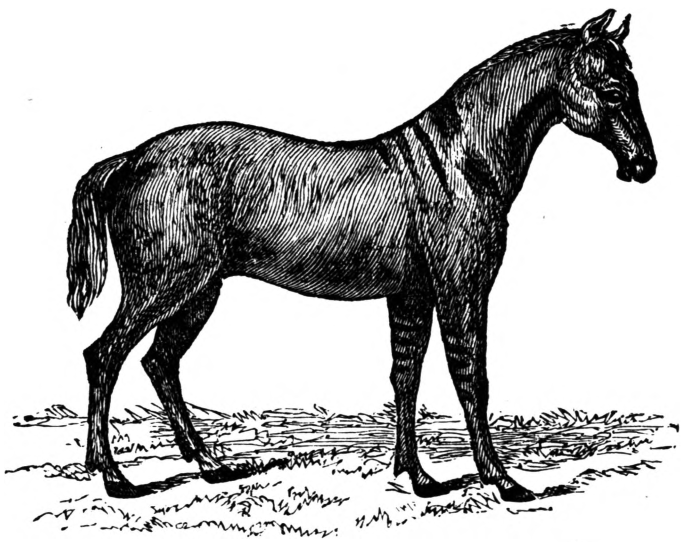

FIG. 25.—Devonshire pony, showing the occurrence of stripes. (From Darwin.)

dark-coloured child may be born in a family where there has been some Eurasian mixture. Cultivated flowers and vegetables, such as pansies and cabbages, sometimes produce forms hardly distinguishable from their wild progenitors. The nectarine derived from a peach may produce what is practically a peach again. The white-flowering currant—derived from the common red form—may have branches with red flowers. These are preliminary illustrations of what are usually called reversions—the hypothesis implied being that they are returns, or "throw-backs," to an ancestral type.

§ 2. *Suggested Definitions*

Darwin's introductory exposition (1868, vol. ii. p. 28) was as follows: "When the child resembles either grandparent more

closely than its immediate parents, our attention is not much arrested, though in truth the fact is highly remarkable; but when the child resembles some remote ancestor, or some distant member in a collateral line—and we must attribute the latter case to the descent of all the members from a common progenitor—we feel a just degree of astonishment. When one parent alone displays some newly acquired and generally inheritable character, and the offspring do not inherit it, the cause may lie in the other parent having the power of prepotent transmission. But when both parents are similarly characterised, and the child does not, whatever the cause may be, inherit the character in question, but resembles its grandparents, we have one of the simplest cases of reversion."

"The most simple case of reversion—namely, of a hybrid or mongrel to its grandparents—is connected by an almost perfect series with the extreme case of a purely bred race recovering characters which had been lost during many ages; and we are thus led to infer that all the cases must be related by some common bond" (*ibid.* p. 49).

"By the term reversion," Weismann says, "is meant the appearance of characteristics which existed in the *more remote* ancestors, but were absent in the *immediate* ancestors—*i.e.* the parents" (1893, p. 299).

Prof. Karl Pearson defines a *reversion* as "the full reappearance in an individual of a character which is recorded to have occurred in a *definite* ancestor of the same race," and *atavism* as "a return of an individual to a character not typical of the race at all, but found in allied races supposed to be related to the evolutionary ancestry of the given race. . . . In reversion we are considering a variation, normal or abnormal, from the standpoint of *heredity in the individual*; in atavism we are considering an abnormal variation from the standpoint of the *ancestry of the race*." But as the two words have been used by some authors in the converse way, and as it is surely difficult to define the field of abnormal variation, we adhere to Darwin's wider usage, and drop the term "atavism" as an unnecessary synonym.

"Reversion," De Vries says, "means the falling back or returning to another type, and the word itself expresses the idea that this latter type is the form from which the variety has arisen. . . . Atavism or reversion is the falling back to a prototype"—*i.e.* "those ancestors from which a form is known to have been derived." But De Vries distinguishes sharply between true reversion due to a

sudden reassertion of latent ancestral characters in a pure-bred stock, and false reversion or vicinism due to crossing. Descriptively both may be called "reversions," but they differ in their nature and their causes. He also distinguishes reversion to a known ancestor from "systematic atavism" to ancestors which are only reputed to be such on taxonomic grounds.

"Reversion," Prof. Bateson points out, "occurs when the sum-total of the factors returns to that which it has been in some original type. Such a return may be brought about by the omission of an element or elements, or by the addition of some missing element needed to complete the original type. Reversion on crossing is thus the particular case in which one or more missing factors are brought in by the parents of the cross-bred." This is the Mendelian interpretation of reversion, and Mr. Bateson does not believe that there are any reversionary phenomena which do not admit of this interpretation.

We would use the term "reversion" to include all cases where, *through inheritance*, there reappears in an individual some character or combination of characters which was not expressed in his immediate lineage, but which had occurred in a remoter but not hypothetical ancestor. We say "*through inheritance*" in order to exclude those cases where the reappearance can be accounted for in some other way. There is no reason for complicating the idea by calling the reversionary character "abnormal," for abnormality is often difficult to define.

If we can arrange a series of related types on an inclined plane in order of their evolution, with the most recent highest up, we can imagine the offspring of one of the highest slipping back (as regards one or several of its characters) to a lower level—slipping back beyond the grade represented by its own family or stock, slipping back out of its species-grade altogether, and so forth. These "throw-backs" might be described as family-reversions, stock-reversions, species-reversions, and so on.

§ 3. *Theoretical Implications*

The general idea behind the term "reversion" is that particular features characteristic of an ancestor may lie dormant—*i.e.* unexpressed in development—for generations, and may suddenly reassert themselves.

In the mosaic which composes an inheritance there may be included items of ancient origin which can lie latent generation after generation, remaining unexpressed in development for lack of the appropriate liberating stimulus, or for other reasons. Certain potentialities or initiatives, which really form part of the inheritance and are really transmitted from generation to generation, may be kept under by other components of the inheritance, or in some way prevented from asserting themselves. At length, in the reconstitution which is associated with the maturation and fertilisation of the germ-cells, or in the intimate germinal struggle which is possibly always going on amongst the diverse hereditary items, the long-latent items find their opportunity and the result is a reversion due to the reassertion of long-latent characters.

The garden of a shepherd's cottage swallowed up in a deer-forest lost all trace of its previous cultivation and became a weed-ground. After many years it was delved, and soon there appeared many different kinds of old-fashioned flowers whose seeds had lain dormant for several generations. So may ancient flowers and weeds now and again reappear out of latency in that garden which we call our inheritance.

So far the old view—a hypothetical interpretation which may hold good in certain cases, such, perhaps, as the appearance of a fourth toe on a guinea-pig's hind foot, or of horns in a hornless race of cattle. What is the new view, which rests on a definite experimental basis? It is briefly as follows. In establishing domesticated or cultivated varieties, man seems to have been for the most part assisting in the "unpacking" of the extremely complex inheritance of the wild type. Thus the colour-varieties of the domestic rabbit are the results of analysing out in varying measure and mixture that beautiful synthesis of hues which we see in the wild rabbit. When certain colour-varieties are crossed and the offspring are of the wild type, this is due to "repacking." Colour-factors which have been separated out by analysis come

together again and restore the wild form. There has been no mysterious re-awakening of long-latent characters. We may still call what occurs a "reversion," but in cases like the above our interpretation is no longer Darwinian.

§ 4. *Phenomena sometimes confused with Reversion*

It is impossible to read the fairly abundant literature without recognising that many phenomena are labelled "reversions" on the flimsiest of evidence. Let us try to make the conception more definite by criticism and elimination of alleged instances. In this criticism we have especially to bear in mind that the term "reversion" is not merely descriptive of the *direction* which the variation takes; it implies that this direction—ancestor-wards—is due to something that occurs in the early history of the germ-cells.

Arrests of Development.—Though popular travesties have reduced a luminous idea to an absurdity, it remains in a general way true that the individual development, especially in the stages of organ-forming, is in some measure a recapitulation of the racial history. Although it is more picturesque than accurate to speak of "every animal climbing up its own genealogical tree," there is a suggestive general resemblance between the stages in the individual development of organs, such as heart, brain, and kidneys, and the stages in the supposed racial evolution of the same.

Now, it not infrequently happens that the recapitulation is notably incomplete, that the development of an organ stops before the normal "finished form" has been attained.

Through defective nutrition or other untoward conditions of nurture, the expression of the inheritance is inhibited. The organism is not able to perfect itself in all its parts; not, we suppose, through any germinal defect (as subsequent generations may show), but simply because it was not sufficiently fed, or

because it was poisoned, and so forth. The results may be congenital, but they are not germinal; they are due to defects not in nature, but in nurture. Thus children born in times of famine are sometimes far below the normal human standard, but it is an assumption to ascribe their deficiencies to their inheritance. In short, all cases of arrested development which can be referred to peculiarities of pre-natal or post-natal nurture should be eliminated from the category of "true inborn reversion." For practical purposes, in rough-and-ready description, they may be called reversions, but they are *modificational* results; they do not require the hypothesis of the reawakening of latent ancestral characters. It is reducing scientific terminology to an absurdity to describe as a reversion what may be simply due to premature birth or deficient nutrition.

There is a stage in the development of the human fœtus when the openings of the nostrils communicate down the lip with the corners of the mouth-opening; when this communication, which is normally closed up, persists, we have (in part) the abnormality known as "hare-lip," normal in rabbit and hare. But there is no reason to interpret the abnormality in man as a reversion; it is an arrest at a stage which is normally passed through; it is probably due simply to a lack of developmental vigour, or more simply still to a lack of adequate nutrition. Dr. Joseph Bell * refers to a case mentioned by Prof. Haughton of young lion-cubs which all died of hare-lip—the supposed reason of the arrest being that the keeper fed the pregnant lioness on tit-bits, without bones. When the supply of bones was ensured on subsequent occasions, the tendency to hare-lip disappeared. In connection with human affairs and qualities of mind and character, it is well to bear in mind that what we call defectives and criminals may *sometimes* be just like these hare-lip cubs, though more viable.

In a hornless breed of cattle, derived originally from a horned breed, a calf is born with small horns. This may be plausibly interpreted as a reversion to a horned ancestor. But when a calf

* "Discussion on Heredity in Disease," *Scottish Med. and Surg. Journ.* vi. 1900, p. 307.

is born with a three-chambered heart, it is gratuitous to call this a reversion to the saurians with three-chambered hearts, from which mammals evolved. It is simply a case of arrested development.

Vestigial Structures.—It is a familiar fact that structures of ancient origin and erstwhile importance may still linger in dwindled expression in organisms where they do not seem to have much or any significance. They are relics of the past, vestiges of ancestral history, comparable, as Darwin said, to the unsounded letters in many words, the *o* in leopard, or the *b* in doubt—non-functional vestigial letters of which the spelling-reformers would rob us so ruthlessly.

Each one of us is a walking museum of such relics, some of which we should probably do better without. Thus the unused muscles of the ear and the rudimentary third eyelid are ancestral characters which persist in us, though without much significance now. They are like the unused, often unusable, buttons, etc. which survive on some parts of our every-day attire—useless, but interesting, vestiges of bygone days. The gill-clefts of reptiles, birds, and mammals; the embryonic teeth of whalebone whales; the buried remains of pelvis and hind-limbs in whales; the hint of a gill in the skate's spiracle, and so on, are familiar examples of these "vestigial structures," traces of ancestral history, and intelligible on no other theory.

But it goes without saying that as the occurrence of these vestigial structures is still normal, there is no utility in calling them "reversions"—even if now and again they are expressed in greater strength than usual or persist beyond the time at which many of them (*e.g.* all the gill-clefts save one) disappear—namely, during development. They are very interesting, however, (1) in showing that ancestral features have great power of hereditary persistence, and (2) inasmuch as they often show great variability.

Acquired Modifications resembling Ancestral Characters.—When an individual exhibits a structural peculiarity not ex-

pressed in parents or grandparents, but known to occur in more or less remote ancestors, we must try to discover how far this peculiarity is *really part of the inheritance.* That is to say, we must inquire whether it may not be a modification induced from without, which happens to resemble an innate character of the ancestors. Many domesticated animals which have become wild (feral) may show features resembling the original wild ancestor, but these may be due to the direct influence of the old environment and the old functions. It is safe to say that many of the so-called reversions of feral animals are not inborn but acquired and modificational.

Filial Regression.—We shall afterwards consider (Chapter IX.) Mr. Galton's Law of Filial Regression, but it must be noticed here, if only to point out that it has nothing to do with reversion. The law, concretely stated, is that offspring are not likely to differ from mediocrity in a given direction so widely as their parents do in the same direction. There is a continual tendency to sustain a specific average, or a stock-average.

Let us take a simple instance from Prof. Karl Pearson's *Grammar of Science.* Suppose a group of fathers with a stature of 72 in.: the mean height of their sons is 70·8 in.—a regression towards the mean height of the general population. On the other hand, fathers with a mean height of 66 in. give a group of sons of mean height 68·3 in.—again nearer the mean height of the general population. The "regression" works both ways; there is a levelling-up as well as a levelling-down. "The father with a great excess of the character contributes sons with an excess, but a less excess of it; the father with a great defect of the character contributes sons with a defect, but less of it."

Now this very important and normal fact of filial regression has nothing to do with reversion, which implies the reappearance of a definite ancestral character or set of characters which have "lain latent" for several generations.

Independent Variations resembling Reversions.—If we

mean by reversion the re-expression of an ancestral character after a period of latency, it is obviously a particular mode of inheritance. From another point of view it is a variation, and due to some unknown germinal conditions which permit a long-latent, but never lost, character to re-assert itself. When we consider the intricate reductions which occur in the maturation of the germ-cells, and the not less intricate reinforcements involved in amphimixis, it is not impossible to imagine how an ancient latent character may come to the front again after many generations.

But we have also to remember that, apart from reassertions of what is relatively old, there is a continual emergence of what is relatively new. What occurred once as a new variation may occur again, and it is a certain fact that the same type of variation occurs over and over again in varieties of different species. How many red and blue flowers have white varieties! how many trees have weeping varieties! how many Arthropods show similar increase or decrease in the number of their joints! how many birds show albinism! There are limits to the variations of the kaleidoscope, and to the kaleidoscope of variations. Therefore it is always possible that a variation really occurring *de novo*, and apart from latent characters, may happen to coincide with an ancestral trait. It may be *described* as a reversion, but it is really an independent variation.

Supernumerary mammæ occasionally occur in human beings in both sexes. Ammon found them in 3 per cent. of German recruits. They obviously *suggest* the several pairs of mammæ which occur in many mammals—*e.g.* in the half-monkeys or Lemurs. Weismann (1893, p. 333) says, "They are undoubtedly to be looked upon as reversions to extremely remote characters possessed by our lower mammalian forefathers." But it seems simpler to regard them as independent variations, comparable to many other abnormal multiplications of parts. They happen to suggest bygone conditions, but that is probably all that we are warranted in saying.

Polydactylism in man has been interpreted as a reversion to an

ancestor with more than five digits; but this is illegitimate, for the so-called "heptadactylous ancestor" is a pure myth. Polydactylism in man can only be called a reversion when there is in the family history a previous occurrence of the same abnormality some generations back.

It occasionally happens that a particular part of the skin in man exhibits a mouse-like covering of close-set hair. To interpret this—a mere random variation—as a reversion is credulous in the extreme. It may also be noted, incidentally, that to call the wool-like covering of small hairs (the "lanugo") on the human fœtus a reversion to a hairy ancestor is quite absurd; it is a normal stage in development quite outside the rubric of reversion. It may be an inheritance from a distant past, but it is no more a reversion than the occurrence of a notochord as a constant antecedent to the development of its substitute, the backbone. Similarly the dog's habit of turning round and round before it settles down to sleep may be interpretable in the light of past history, but it has nothing to do with reversion.

"When horses are occasionally born at the present day in which one or two accessory toes are present on two or even all four feet, we are perfectly right in considering the development of these toes to be due to reversion to an ancestor of the Miocene period." That the modern horse which steps daintily on the tip of a single (third) toe for each limb, and has merely hidden rudiments of the second and fourth, has been evolved from a many-toed ancestor, is one of the most certain of evolutionist inferences, but are we "perfectly right" in interpreting the occasional development of supernumerary toes, as on Julius Cæsar's horse, to the reassertion of latent ancestral items in the inheritance? Is it not simpler to regard this as an independent variation, comparable to multiplications of other parts to which reversionary interpretations are inapplicable? We must remember, also, that vestigial organs are in many cases peculiarly liable to vary.

It ought not to be necessary to remark that *the ancestor to whom the organism is supposed to revert must be real, not hypothetical.*

Some enthusiastic exponents of the reversion theory have not scrupled to name or even invent the ancestor to whom the

peculiarity in question is supposed to be a reversion, although evidence of the pedigree is wanting. And the terribly vicious circle is not unknown of arguing to a supposed ancestor from the supposed reversion, and then justifying the term "reversion" by its resemblance to the supposed ancestor. Playing with biology can hardly go further than this! Moreover, the postulate of characters remaining latent (save for occasional more or less hypothetical reawakenings) for millions of years, is made as glibly as if it were just as conceivable as a throw-back to a great-grandfather.

There are many reasons why it is absurd to describe a Cyclopean one-eyed human monster as a reversion to the one-eyed larval ascidian. One is that there is no warrant for believing that the ascidian type was in the direct line of our long pedigree.

One of the diagnostic features of gout is the presence of uric acid in the blood, and its deposition in various tissues of the body (doubtless helped by the frequently associated degeneration of the kidney, which is normally competent to filter out the normal nitrogenous waste-product, which is mostly in the form of urea). It is known, however, that reptiles, for instance, like many backboneless animals, normally excrete most or a large part of their nitrogenous waste in the form of uric acid. This has led even such an eminent pathologist as Prof. Hamilton (1900, p. 297) to say, "May we not entertain, as a possibility, that the gouty constitution, so-called, is in part a reversion to some far-back ancestor, in which uric acid was excreted normally to a much larger extent than it is at present in an average member of the human race?" That is to say, the gouty person reverts to the physiological habit of a far-back ancestral organism (not even any known mammalian type), which had uric acid as a characteristic waste-product, but he does not, unfortunately, revert to the associated condition of having kidneys able to excrete the uric acid adequately. But our simple point is that the supposition of gouty tendencies lying *latent* in some form or other through literally millions of years taxes our imagination too severely. Such instances are almost sufficient to damn the reversion hypothesis altogether.

§ 5. "*Skipping a Generation*"

It is often remarked in human inheritance that a child re-exhibits the peculiarity of a grandfather or grandmother, which the parents did not show. A Mendelian interpretation of this is in some cases possible. "If the two grandfathers have blue eyes and both grandmothers brown eyes, then the parents may both have simplex brown eyes * ; they will both form germ-cells of which 50 per cent. have and 50 per cent. lack the determiner to form brown iris pigment. From such brown-eyed parents one child in four will have blue eyes like the grandfathers. This is atavism. Cases of atavism can, in general, be explained on the same ground as atavism to blue-eyed grandparents" (Davenport, 1910, p. 292).

In case of sex-limited characters, such as bleeding or hæmophilia, the phenomenon of "skipping a generation" may be illustrated. For the hæmophilia is usually transmitted through unaffected daughters to grandsons. This may be comparable to other cases of sex-limited inheritance, *e.g.* in certain strains of sheep where the horns are confined to the males.

It is likely that skipping a generation is less frequent than it is supposed to be; thus features which the parent thinks he never had may have been plain enough when he was of the same age as his son now is. Moreover, in the case of characters that blend it is an obvious possibility that a grandson should sometimes show his grandfather's pattern. Finally, some cases of the disappearance of exceptional ability and the return to mediocrity come within the rubric of "filial regression."

But our present point is that there seems little utility in calling "skipping a generation" a "reversion," or even an atavism.

A drone-bee arises from an unfertilised egg; it has a mother and two grandparents, but no father. But it seems rather absurd to call its resemblance to its grandfather either atavistic or reversionary. This is a *reductio ad absurdum*, for the drone-bee would resemble its father if it had one!

* "Ordinarily when parents are similar, each unit character of the offspring develops from two similar determiners—one paternal and one maternal. Thus in its origin any unit character is duplex. When, however, the determiner is found in only one of the parents the character is simplex." This will be clearer after the chapter on Mendelism has been read.

§ 6. *Mendelian Interpretation of Reversion*

As we have already indicated, the number of alleged reversions has been greatly reduced by the results of the study of Mendelian inheritance. An interesting re-interpretation of "reversions" has been supplied.

Some red guinea-pigs, as Castle has shown, produce in crosses with a black race the "agouti" type of coat found in all wild guinea-pigs, and various experiments prove that this is due to the coming together of three colour-factors—simple red, simple black, and a third which is carried by the red but can become visible only in the presence of both black and red.

In certain instances, which are quite well defined by the Mendelian experimenters, a cross between a black and an albino mouse, or between a black and an albino rabbit, results in a complete reversion to the wild grey form.

Crosses between the tall, upright, bush-like "Bush" sweet-pea and the dwarf prostrate "Cupid" variety resulted in a procumbent plant with long internodes, like the wild type that is found growing in Sicily.

In these and in similar cases it has been possible by various experimental tests to give convincing proof that the reversion is a re-synthesis of characters that had been analysed apart. As Prof. R. C. Punnett concludes: "Reversion, therefore, in such cases we may regard as the bringing together of complementary factors which had somehow in the course of evolution become separated from one another" (1911, p. 54).

§ 7. *Reversion in Crosses*

False Reversion or Vicinism.—In his criticism of cases which have been labelled "reversions," De Vries draws a sharp distinction between "true reversion," due to unknown internal causes which induce long-lost latent ancestral characters to assert themselves, and "false atavism or vicinism," which is due to crossing. His investigation of a large number of cases led him

to conclude that "true atavism, or reversion caused by an innate latent tendency, seems to be very rare," and that most of the botanical instances are due to crossing. He calls this false reversion "vicinism," as indicating the sporting of a variety under the influence of others in its vicinity. "Crossing and pure variability are wholly distinct groups of phenomena, which should never be treated under the same head, or under the same name." He does not deny in any way the numerous "reversions" which gardeners describe; he simply points out (with much circumstantial evidence to warrant his contention) that nearly all these ordinary "reversions" are due to crosses. He shows, for instance, how a famous case, the reversion of the "Tuscarora" variety of American corn cultivated by Metzger in Baden, may be readily interpreted as a typical instance of *vicinism*. Why the offspring of hybrids should revert to the parental type is another question, to which we shall return in the chapter on Mendelism (Chapter X.).

Two white-flowered sweet-peas are crossed, and the result is a progeny with the wild, purple flowers. Two smooth stocks are crossed, and the result is a progeny with the original hoary, ancestral type. These cases are what Darwin called "reversion on crossing." But, as Mr. Bateson says, "such reversion is nothing but the meeting of two parted complementary elements, which have somehow been separated by variation."

Thus it is possible that many so-called reversions may be simply Mendelian phenomena in disguise.

§ 8. *Reversion of Retrogressive Varieties*

Within a species it is often possible to distinguish several subspecies or "elementary species" (De Vries), which differ from one another in many characters affecting many organs. Thus in the species called *Draba verna*, or whitlow grass, there are two hundred or so minor groups, like constellations within

constellations. But the species may also include "varieties," more or less sharply distinguished from the rest of the species by the apparent absence of some notable specific feature, or, more rarely, by the acquisition of some peculiarity already seen in closely allied species. They stand aside, as it were, like far outlying parts of the constellation. "Varieties," thus defined, usually differ from their parent species in a single sharp character only, or in several correlated characters; they usually arise in a negative way by the apparent loss of some quality; and they have great stability. They are comparable to the familiar colour-varieties in rabbits, guinea-pigs, mice, etc., which seem to arise by the dropping out of part of the ancestral equipment of characters. They are in no sense reversions.

Illustrations.

White "varieties" of red and blue flowers—*e.g.* of red-flowering currant.

Smooth "varieties" of hairy plants—*e.g.* nectarine (from peach).

Smooth "varieties" of prickly plants—*e.g.* holly and gooseberry.

Rayless "varieties" of many composites normally with ray florets—*e.g.* white marigold, camomile, daisy.

Radiate "varieties" of many composites, normally with no ray-florets—*e.g.* tansy and groundsel.

Red "varieties" of white flowers—*e.g.* hawthorn.

Red "varieties" of green trees and shrubs—*e.g.* beech and birch.

Weeping "varieties" of ash, willow, etc.

Starchless seeds—*e.g.* sugar-corn.

Seedless fruits—*e.g.* banana and mandarin orange.

Mr. Burbank's stoneless plum.

As these varieties are most frequently in a negative direction having apparently lost some character which their parent-species possesses, De Vries includes most of them in the term "retrograde varieties." Perhaps "retrogressive varieties" would be a clearer term.

They usually breed true, but some of them are perpetuated asexually—*e.g.* of course, the seedless fruits. Sometimes, however, the apparently lost ancestral character re-appears, as when the smooth nectarine, a "variety" of peach, becomes

downy, or when the white-flowering currant puts forth red flowers. Such cases may be described as reversions to the specific type, and they can be interpreted only in two ways. Either we have to do with new variations which happen to hit the old mark, or, as seems more probable, latent ancestral characters have re-asserted themselves.

It is a current belief that these "varieties" have a strong tendency to "revert" to the parent species, but, according to De Vries, this is, as regards pure varieties, not of hybrid origin, and ordinarily propagated by seeds, a popular delusion. "In the present state of our knowledge it is very difficult to decide whether or not true reversion occurs in constant varieties. If it does occur it surely does so very rarely, and only under unusual circumstances, or in particular individuals" (1905, p. 155). It must be noticed, however, that De Vries distinguishes true reversion (due to a spontaneous germinal change) from false reversion which is induced by hybridising.

In illustration of the constancy of varieties he cites the wide-spread rayless form of the wild camomile (*Matricaria chamomilla discoidea*), which is so constant that many botanists have made a species of it. De Vries raised in successive years between 1,000 and 2,000 seedlings, but observed no trace of reversion. Similarly, the rayless "variety" of the common tansy ragwort (*Senecio jacobæa*) is quite as stable as the radiate species. De Vries also refers to the stability of white strawberries, green grapes, white currants, crisped lettuce, crisped parsley, smooth spinach, white flax, sugar-corn, and strawberries without runners.

Seed-reversion very Rare.—Excluding cases where it is doubtful whether the variety has not a hybrid origin, and is therefore liable to the peculiar phenomenon known as the splitting up of hybrids, excluding also all cases of "sporting varieties," where an apparent reversion might be a mere coincidence in the crowd of variations, De Vries concludes that "seed-reversions must be said to be extremely rare. . . .

It would be bold indeed to give instances of seed-atavism, and I believe that it will be better to refrain wholly from doing so. . . . It is by far safer in the present state of our knowledge to accept bud-variations only as direct proofs of true atavism. And even these may not always be relied on, as some hybrids are liable to split up in a vegetative way, and in doing so to give rise to bud-variations that are in many respects apparently similar to cases of atavism" (1905, p. 176).

§ 9. *Interpretations in Terms of Reversion*

As in many other cases, one of the difficulties in regard to the reversion theory is that in terms of it much can be interpreted and relatively little demonstrated. In regard to the origins of domesticated animals and cultivated plants, we remain in great obscurity. In regard to the actual pedigree of wild species our ignorance is even greater. Thus, while it is often easy to interpret an unexpected variation as a reversion to a plausible ancestral type, we have little security in so doing.

Thus De Vries distinguishes between experimentally demonstrable reversion and what he calls "systematic atavism," where the ancestral type is merely presumed to be so-and-so on the basis of taxonomic considerations.

It is probable that the common ancestors of the "elementary species" (*Primula officinalis*, *P. elatior*, and *P. acaulis*), which make up the systematic species of primrose, *Primula vera*, were "perennial plants with a rootstock bearing their flowers in umbels or whorls on scapes. Lacking in *Primula vera*, these scapes must obviously have been lost at the time of the evolution of this form." But in the common acaulescent "elementary species," *P. acaulis*, a scape sometimes develops. It may be reasonably *interpreted* as due to the re-vitalising of a dormant scape-character inherited from the presumed ancestor. "Similarly with the appearance of bracts in the usually bractless

Crucifers, and with the unexpected appearance of *upright* tomatoes. Similarly, the twisted teasels lose their decussation, but in doing so the leaves are not left in a disorderly dispersion, but a distinct new arrangement takes its place, which is to be assumed as the normal one for the ancestors of the teasel family."

§ 10. *Further Examples of Reversion*

In one of Prof. Cossar Ewart's experiments a pure white fantail cock pigeon, of old-established breed, which in colour had proved itself prepotent over a blue pouter, was mated with a cross previously made between an owl and an archangel, which was far more of an owl than an archangel. The result was a couple of what were, theoretically, fantail-owl-archangel crosses, but the one resembled the Shetland rock-pigeon, and the other the blue rock of India. Not only in colour (slaty-blue), but in shape, attitude, and movements there was an almost complete reversion to the form which is believed to be ancestral to all the domestic pigeons. The only marked difference was a slight arching of the tail, but there were only twelve tail-feathers, as in the rock-dove, whereas the father fantail had thirty.

A dark bantam hen, crossed with an Indian game Dorking cock, produced amongst others a cockerel almost identical with a jungle fowl (*Gallus bankiva*)—*i.e.* with the original wild stock (Ewart).

Similarly, in his horse-zebra hybridisations, Ewart obtained forms whose stripings were at least plausibly interpreted as reversions to an extremely old type of horse, such as is hinted at in the striped ponies of Tibet.

A smooth-coated white rabbit, derived from an Angora and a smooth-coated white buck, was mated with a smooth-coated, almost white doe (grand-daughter of a Himalaya doe), with very interesting results, significant of the complexity of

the conditions. In the litter of three, one was the image of the mother, one was an Angora like the paternal grand-

FIG. 26.—Varieties of domestic pigeon arranged around the ancestral rock-dove (*Columba livia*). (Based on Darwin's figures.)

mother, and the third was a Himalaya like the maternal great-grandmother.

For all these cases, except that of the horse-stripings, as also for similar cases given by Darwin, Mendelian interpretations are now forthcoming, and the hypothesis of the re-assertion of long latent ancestral characters is unnecessary.

When the swimming-bell or medusoid *Epenthesis folleata* appears with pentamerous symmetry instead of the usual arrangement of its organs in fours or multiples of four, no one would dream of calling this discontinuous variation an instance of *reversion*, for we only know of one medusoid (*Pseudoclytia pentata*) where five is normally the ruling number (Mayer, 1901). But when the last-named medusoid occurs with four oral lips, as it occasionally does, it may be said that this variation is reversionary, since there is good reason to believe that *Pseudoclytia pentata* is a pentamerous derivative of the *Epenthesis* stock. Even in this case the interpretation of the four lips as reversionary may not be correct, since, as a matter of fact, the number of lips in *Pseudoclytia* varies from one to seven.

Reversion in Parthenogenesis.—Weismann (1893, p. 344) reports a very interesting case which he observed in varieties of a small Ostracod crustacean (*Cypris reptans*) which multiplies parthenogenetically. In the course of observations extending over eight years he found that, amidst the expected uniformity of resemblance between parent and offspring, exceptions occasionally occurred. These were of such a nature that he could only interpret them "as exhibiting reversions to an ancestral form many generations removed."

Other Instances of Reversion

White-flowering Currant.—The white-flowering variety of the red-flowering currant (*Ribes sanguineum*) is said to have originated many years ago from seed in Scotland. "Occasionally this white-flowered currant reverts back to the original red type, and the reversion takes place in the bud. . . . Once reverted, the branches remain for ever atavistic. It is a very curious sight, these small

groups of red branches among the many white ones" (De Vries, 1905, p. 167). This case is peculiar, however, because the white variety is propagated only by cuttings or grafting. "If this is true, all specimens must be considered as constituting together only one individual, notwithstanding their wide distribution in the gardens and parks of so many countries. This induces me to suppose that the tendency to reversion is not a character of the variety as such, but rather a peculiarity of this one individual" (p. 168).

Wheat-ear Carnations.—Large beds of carnations sometimes show peculiar anomalous forms known as "Wheat-ears," with small green ears instead of flowers. There has been a loss of flowers and a multiplication of bracts. On a specimen of this De Vries observed that some branches reverted wholly or partially to the production of normal flowers. "The proof that this retrograde modification was due to the existence of a character in the latent state, was given by the colour of the flowers. If the reverted buds had only lost the power of producing spikes, they would evidently have returned to the characteristics of the ordinary species, and their colour would have been a pale pink. Instead of this, all flowers displayed corollas of a deep brown. They obviously reverted to their special progenitor, the chance variety from which they had sprung, and not to the common prototype of the species" (1905, p. 229).

A Picturesque Case.—The long-headed green dahlia originated twice from two different double-flowered varieties—a deep carmine with white tops on the rays, and a pale orange known as "Sunrise." They were quite sterile and were progagated asexually, one in Prof. De Vries's garden, the other in the nursery at Haarlem, where both arose. "In the earlier cultures both remained true to their types, never producing true florets. No mark of the original difference was to be seen between them." But in 1903 both reverted to their prototypes, and bore ordinary double flower-heads. "Thus far we have an ordinary case of reversion. But the important side of the phenomenon was, that each plant exactly 'recollected' from which parent it had sprung. All of those in my garden reverted to the carmine florets with white tips, and all of those in the nursery to the pale orange colour and the other characteristics of the 'Sunrise' variety" (1905, p. 231). It seems impossible not to admit that characters of the parent-varieties had lain for a time latent and had eventually reasserted themselves.

Conclusion.—In his *Locksley Hall Sixty Years After* Tennyson spoke of—

> Evolution ever climbing after some ideal good,
> And Reversion ever dragging Evolution in the mud;

but this is making a bogey of reversion. Many of the phenomena commonly labelled as "reversions" are wrongly labelled, and true Reversion does not seem to be of frequent occurrence. Moreover, when it does occur, it may mean, not a deterioration, but a return to a position of greater organic stability. What acts as a drag or brake—often advantageously—on progressive variation is not so much reversion as *filial regression.*

But the great step of progress that has been made of recent years is due to the Mendelian experimenters who have shown that many of the reversions which follow crossing are due to the re-combination of complementary factors which had become separated in the course of domestication and cultivation.

Wherever this can be shown there is, of course, no warrant for the hypothesis that reversion is due to the sudden activation of a long latent ancestral character. But this hypothesis may be in the meantime retained for any cases that appear to demand it,

CHAPTER VI

TELEGONY AND OTHER DISPUTED QUESTIONS

"The mysterious wireless telegraphy of ante-natal life."—J. W. BALLANTYNE.

§ 1. *What is meant by Telegony.*
§ 2. *The Classic Case of Lord Morton's Mare.*
§ 3. *Representative Alleged Cases of Telegony.*
§ 4. *Ewart's Penycuik Experiments.*
§ 5. *Suggestions which explain away Telegony.*
§ 6. *Suggestions as to how Telegonic Influence might be effected.*
§ 7. *A Statistical Suggestion.*
§ 8. *The Widespread Belief in the Occurrence of Telegony.*
§ 9. *An Instructive Family History*
§ 10. *A Note on Xenia.*
§ 11. *Maternal Impressions.*

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§ 1. *What is meant by Telegony*

THE term "telegony" is applied to doubtful, certainly rare, but, if true, very remarkable cases where an offspring resembles a sire which, though not its father, had previously paired with its mother. More theoretically expressed, telegony is the supposed influence of a previous sire on offspring subsequently borne by the same female to a different sire. The ovum or the embryo is supposed to be influenced by the mother's previous impregnation or by the consequences thereof.

To take a simple instance, the racehorse Blair-Athol had a very characteristic blaze or white bald face, and it is said that mares which had once borne foals to Blair-Athol subsequently produced to quite different stallions foals which exhibited the Blair-Athol blaze. It is very generally asserted by dog-breeders that if a thorough-bred bitch has had pups to a mongrel, her value is greatly decreased, for she will not afterwards breed true.

The alleged phenomena are of much interest, but the evidence of their actual occurrence is far from satisfactory, and their theoretical interpretation in terms of telegony is beset with physiological difficulties. But as a belief in telegony is still widespread, it will not be unprofitable to consider (*a*) the alleged facts, and (*b*) the interpretations suggested.

§ 2. *The Classic Case of Lord Morton's Mare*

The classic case, given by Lord Morton (1821), is thus summarised by Darwin : " A nearly purely bred, Arabian, chestnut mare bore a hybrid to a quagga ; she was subsequently sent to Sir Gore Ouseley, and produced two colts by a black Arabian horse. These colts were partially dun-coloured, and were striped on the legs more plainly than the real hybrid, or even than the quagga. One of the two colts had its neck and some other parts of its body plainly marked with stripes. Stripes on the body, not to mention those on the legs, and the dun-colour, are extremely rare—I speak after having long attended to the subject—with horses of all kinds in Europe, and are unknown in the case of Arabians. But what makes the case still more striking is that the hair of the mane in these colts resembled that of the quagga, being short, stiff, and upright. Hence there can be no doubt that the quagga affected the character of the offspring subsequently begot by the black Arabian horse" (Darwin, 1868, vol. i. pp. 403-4).

In 1823 the mare had again a foal by an Arab stallion, and this also showed some quagga characters.

It may well be asked: If this was not telegony, what was it? But the case is not quite so satisfactory as it seems. Settegast * remarks that the drawing made of the foal with the alleged quagga characters merely shows indistinct dark stripes on the neck, withers, and legs, and that similar stripes not uncommonly occur on pure-bred foals. A stiff mane may also occur as a variation in horses. It is possible that the alleged quagga-like characters had nothing to do with the original quagga sire, but were reappearances of latent ancestral characters.

Sanson (1893) sets another case against Lord Morton's. A bay mare had by two different stallions seven foals of a uniform colour, and then by a third stallion a foal *more* zebra-like than Lord Morton's. To which Delage adds that this eighth foal was pommelled grey—a colour with which zebra-like stripes are not infrequently associated.

Cornevin cites a breeder from the Pyrenees to the effect that a mare served by an ass and producing a mule was thereafter served by a horse and cast a foal which had hoofs more mule-like than horse-like. But this is too vague to be of much use, and besides, "asinine" variations sometimes occur in horses where there has been no hybridising (Sanson, 1893).

Moreover, the opposite result has been often obtained. Settegast (1888) gives the case of four stud mares which were served by asses and bore mules. They were subsequently served by horses, and the foals showed no asinine traits.

§ 3. *Representative Alleged Cases of Telegony*

Man.—Herbert Spencer cites from Flint's *Human Physiology* (1888) the case of a white woman who had intercourse with a negro and afterwards with a white man. There were some negro-pecu-

* *Thierzucht*, Berslau, Bd. i. 1878, pp. 223-34.

liarities in the children by the second male. But it is perhaps enough to say that it is difficult to get at the truth in such cases.

Cornevin (1891, p. 356) gives the following case. The widow of a hypospadic man had by a second and normal husband four hypospadic sons, two of whom transmitted the abnormality (*Lancet*, 1884). But in a case like this we require further particulars—*e.g.* as to the normality of the mother, and as to any tendency to hypospadism both in her ancestry and in that of her second husband.

Cornevin also cites the case of a woman married to a deaf-mute, by whom she had one deaf-mute child. By a second normal husband she had a deaf-mute child, and then others who were normal (Ladreit de Lacharrière, in preface to Goguillot's *Comment on fait parler les sourds-muets*, Paris, 1889). But here again it is necessary to know whether there was any tendency to deaf-mutism on the mother's side or in the ancestry of her second husband.

Dogs.—It is the deeply rooted opinion of dog-breeders—doubtless resting on a basis of experience, though it may be misinterpreted experience—that a bitch of good stock once lined by a mongrel is spoilt for further prize-breeding. It is said that many valuable bitches have been sacrificed because of this deeply rooted opinion.

The following case is cited by Cornevin (1891, pp. 356-7), from Kiener (1890). An Artesian bitch was first lined by a wall-eyed mastiff, and afterwards by an Artesian dog. Among the pups born to the latter one was wall-eyed. One requires to know how frequently a wall-eyed variation crops up, and whether there was any occurrence of it in the ancestry of the mother or of the second male.

Darwin (1868) gives the case of a hairless Turkish bitch which was lined by a spaniel, and had some hairless pups and some with short hair. She was subsequently paired with a hairless Turkish dog, but the offspring were as before. It must again be asked whether there may not have been some spaniel strain in the previous ancestry.

Spencer (1893) tells of a Dachshund bitch which was paired with a collie and had a hybrid litter. The following year she bore to a Dachshund a similar hybrid litter. But we require to know how thoroughly pure-bred the Dachshund mother and father were.

Perhaps the most useful comment on the cases of reported telegony in dogs is that made by Prof. Cossar Ewart (1901): "When it is remembered that we are surprisingly ignorant of the origin of the various breeds of dogs, and that, however pure the breed, reversion

to a former ancestor may at any moment occur, it will, I think, be admitted that, for the purpose of testing the 'infection' doctrine, the dog, of all our domestic animals, is the least satisfactory." Mr. C. H. Lane, discussing toy spaniels in his book, *All about Dogs*, says, "I have been told by breeders that they have had in one litter a specimen of all four breeds [*i.e.* of King Charles, Prince Charles, Blenheim, and Ruby spaniels]. In the same way rough and smooth terriers often occur in the same litter, not because of infection, but because of reversion."

Cats.—Dr. H. de Varigny tells of a normal cat which, after producing kittens to a Manx cat, had several tail-less kittens to an ordinary cat (*Journal des Débats*, September 9th, 1897; cited by Ewart, 1901). But the mother, or the second father, or both, may have had a tail-less ancestor, to which some of the kittens happened to revert. Or even if there were no such ancestor, the tail-lessness may have been merely a variation that happened to coincide with the peculiarity of the first sire, but was not in any way due to him. For tail-lessness is not a very rare "sport."

As a counter-case, Prof. Ewart refers to "a pair of young cats, of a somewhat peculiar variety, obtained from Japan. These cats belonged to a small breed, bluish in colour, with the exception of the ears and extremities, which were black. When the female grew up she first had kittens to a common tabby cat. These kittens showed the characteristic tabby markings. Her next kittens were by her Japanese mate, but in no respect did they suggest the previous tabby-coloured mate. No better experiment than this could be made with cats. The imported breed was quite distinct, and yet not sufficiently prepotent to swamp the common domestic English cat. Yet, though the first litter was sired by a common tabby, there was no indication whatever of the previous tabby mate in her second and pure-bred litter." (Case cited by Sydney Villar, F.R.C.V.S., *Proc. Nat. Vet. Assoc.* 1900, p. 130.)

Sheep.—Dr. Alexander Harvey, in a paper "On a Curious Effect of Cross-breeding" (1851), gives on the authority of W. McCombie of Tilliefour, Aberdeenshire, the following case:

Six pure-bred black-faced horned ewes were put, in the autumn of 1844, some to a Leicester ram (white-faced and polled), and others to a Southdown ram (dun-faced and polled), and produced cross-bred lambs:

In the autumn of 1845 the same ewes were put to a pure black-

faced horned ram of their own breed. The lambs were all polled and brownish in the face.

In the autumn of 1846 the ewes were again put to another fine ram of their own breed. Again the lambs were mongrels, but not so markedly as before. Two were polled and dun-faced, with very small horns; while the other three were white-faced, with small round horns. At length the owner parted with his ewes without getting from them a single pure-bred lamb.

Perhaps, however, the ewes were not so pure-bred as was supposed.

Cornevin cites from Magne the statement that white ewes, first crossed by black rams and then by white rams, bear to the latter, lambs which are piebald or which have blackish eyelids, lips, and limbs (Magne, J. H., *Hygiène vétérinaire appliquée*, p. 206). But black variations are common even when no black rams have been used for several generations.

Cattle.—Weismann (1893, p. 385) refers to a case reported by Carneri. A cow of a dark grey Mürzthal herd was put to a "light-coloured Pinzgau bull"; it bore a calf with the characteristic brown and white patches of the Pinzgau breed, as well as with distinct traces of the dark grey Mürzthal cross. It was subsequently served by a Mürzthal bull, and the second calf, while for the most part grey, showed "large brown spots like those of the Pinzgau breed." But this case is also inconclusive, since it is possible, as Carneri admitted, that "a drop of Pinzgau blood" may have previously got into the Mürzthal herd without his being aware of it.

Pigs.—Another circumstantial case cited by Darwin is that of a sow of Lord Western's black-and-white Essex breed, which Mr. Giles put first to a deep chestnut wild boar and after a time to a boar of the black-and-white breed. The offspring of the first union showed the characters of both parents, but in some the chestnut colour of the boar prevailed. From the second union the sow produced some young plainly marked with the chestnut tint, which is never shown by the Essex breed (Darwin, 1868, vol. i. p. 404).

Rodents.—Breeders of rabbits, rats, and mice have sometimes reported phenomena which suggest telegony; but the great variability of these rodents makes them very unsuitable subjects of experiment.

Prof. Cossar Ewart refers to two cases. Mr. C. J. Pound, bacteriologist to the Queensland Government, "crossed a grey rabbit with a grey-and-white buck, and then mated her with a black buck

with the result that in the second litter there were grey-and-white as well as grey-and-black young. Again, a female black rat after breeding with a pure white rat produced, to a brown rat, white, brown, and piebald offspring. . . . Had Mr. Pound made a number of control experiments he would doubtless have discovered that black female rats sometimes yield to a brown rat white, brown, and piebald offspring, without having been first mated with a white rat, and that grey doe rabbits often produce to a black buck grey-and-white as well as grey-and-black young."

Experiments on rats and rabbits made by Dr. Bond (*Trans. Leicester Literary and Philosophical Society*, vol. v. October, 1899) yielded no results which could not be readily interpreted as due to reversion and other forms of variation.

Birds.—A case of supposed telegony in birds is referred to by Darwin (1868, vol. i. p. 405): "A careful observer, Dr. Chapuis, states (*Le Pigeon Voyageur Belge*, 1865, p. 59) that with pigeons the influence of a first male sometimes makes itself perceived in the succeeding broods; but this statement, before it can be fully trusted, requires confirmation." Mr. Frank Finn, in a paper entitled "Some Facts of Telegony" (*Natural Science*, iii., 1893, pp. 436–40), cites a number of cases which seem to him to afford evidence of telegonic phenomena in birds, but they are not convincing.

From the above citations it appears that the evidence of the occurrence of telegony is in great part, at least, of the same unsatisfactory character as that adduced in favour of use-inheritance —largely anecdotal, impressionist, and uncriticised. The need for careful experiments like those begun by Prof. Ewart (1896) is obvious.

§ 4. *Ewart's Penycuik Experiments.*

The position of affairs being that a number of great authorities —*e.g.* Darwin and Spencer—had expressed their belief in the occurrence of telegony, and that a number of equally competent authorities had expressed themselves extremely sceptical on the subject, Prof. Ewart resolved on definite experiment—the only secure path.

In general terms, he made a number of experiments likely

to give telegony the best possible chance of declaring itself, and although he has displayed his scientific mood in abstaining from dogmatic conclusion, and in suggesting many other experiments which should be made, there is no ambiguity in his verdict that the evidence of any undoubted telegony is very unsatisfactory. The Penycuik experiments proved this, at least—that telegony does not generally occur, even when what were considered to be favourable conditions were secured; indeed, anything suggestive of telegony occurred only in a very small percentage of cases. Moreover, where peculiar phenomena of inheritance were observed, they seemed to be readily explicable on the reversion hypothesis.

The general nature of the experiments may be understood by taking one of the best cases, which loses much, however, when summarised apart from the beautiful pictures illustrating the book (Ewart, 1899). A Rum pony mare, Mulatto, of remarkably pure breed, was served by a Burchell zebra stallion, Matopo, and the result in August, 1896, was Romulus, whose markings were quite different from those of his sire, being suggestive rather of the Somaliland zebra. In 1897 Mulatto had a bay colt foal to a grey Arab stallion, and this foal—unfortunately short-lived—gave no proof of telegony. The stripes which most frequently occur in horses were absent; there were others which are not uncommon in horses; but the most distinct markings (not that any were strongly developed)—namely, those across the croup—were of a sort extremely rare in both foals and horses. In short, the markings of Mulatto's second foal were puzzling, but in no definite way suggestive of the influence of the previous zebra sire. In this, as in the other cases, the verdict as to the occurrence of telegony was "non-proven."

In regard to experiments it should be remembered, however, that if telegony (supposing it to be a fact) be due to some strange persistence or unusual influence of the spermatozoa of a previous sire, then many *isolated* cases with negative results do not prove

much. As Pearson observes (1900, p. 462), "should it occur once in a hundred trials we are hardly likely just to hit upon the successful instance."

§ 5. *Suggestions which explain away Telegony*

(*a*) It has been repeatedly suggested, by those who do not believe in the reality of telegonic influence, that the phenomena are simply illustrations of *reversion*. A normal cat has kittens to a Manx cat, and afterwards to a normal cat. In the second litter some are tail-less. "It does not follow, however, that some of the subsequent kittens were tail-less *because* their dam had been previously mated with a cat of the Manx breed. . . . The most likely explanation is that tail-less individuals occurred in the ancestry of one or both of the parents; in other words, the absence of the tail is due to reversion to an ancestor" (J. Cossar Ewart, *Trans. Highland and Agricultural Society of Scotland*, 1901).

This view amounts to denying telegony in the strict sense. We are asked to believe that there is no causal nexus between the previous sire and the subsequent offspring who resemble him. They happen to resemble him because he resembled one of their ancestors. This seems to us easier than believing in telegony.

The plausibility of this explanation will vary in different cases. Thus Finn points out that the occurrence of feather-legged fowls in a pure Dorking breed, or of polled lambs from black-faced horned ewes, cannot be set down to reversion, "feather-legged fowls and polled sheep not being ancestral types."

(*b*) It has also been suggested that the subsequent offspring have accidentally varied in the direction of resemblance to the previous sire. The resemblance is a mere coincidence. As the reliable facts are few and far between, there is much to be said for this view.

(*c*) Another suggestion explains away the alleged facts of telegony by referring them to maternal impression, the supposition being that the mental image, etc., produced in the mother by the first sire exerts an influence on subsequent germs or on their development after fertilisation by another sire. There is little to be said in favour of this interpretation!

§ 6. *Suggestions as to how a Telegonic Influence might be effected*

(*a*) It is well known that in most European bats sexual union usually occurs in autumn, but the spermatozoa are simply stored in the uterus, ovulation and fertilisation taking place in spring after the winter sleep. A somewhat similar retention of stored spermatozoa, which become operative long after impregnation, is familiar in insects: thus, in some queen bees the store has been known to last for two or three years, and Sir John Lubbock gives the remarkable instance of an aged queen ant which laid fertile eggs thirteen years after the last union with a male. From a consideration of such facts the suggestion has emerged that the second offspring are really fertilised by persistent spermatozoa derived from the first sire.

Weismann (1893, p. 385) suggests the possibility that "spermatozoa had reached the ovary after the first sexual union had occurred, and had penetrated into certain ova which were still immature." When these ova mature amphimixis might occur, and coincide in time with a second coitus to which the subsequent offspring would be ascribed.

But were this the explanation, we should sometimes find, as Weismann remarks, that offspring were produced without any second sire at all. No such phenomenon is known among higher animals.

Moreover, there is no warrant for supposing that spermatozoa can persist as such through a period of gestation. "There is abundant evidence," Prof. Cossar Ewart says, "that in the

rabbit, as in other mammals, unused sperms lose their fertilising power and disintegrate long before the period of gestation comes to an end."

For these two reasons the above interpretation may be rejected.

(*b*) Somewhat subtler is the suggestion—often also called the "infection hypothesis"—that although the sperms of the first sire cannot be supposed to persist and fertilise ova discharged long afterwards, yet it is conceivable that the disintegrated substance of the sperms may persist and influence the ovaries and the ova, or that the sperms may exert an influence which does not amount to fertilisation.

So great a physiologist as Claude Bernard seems to have believed in the possibility of such an influence, though it is somewhat suggestive of the "aura seminalis" of the ancients. In this connection, however, Cornevin recalls the facts that a turkey-cock's impregnation of the female suffices for the score or so of fertile eggs which are laid during the season, and that the common cock's act suffices for seven or eight eggs. In both cases the fertile eggs are succeeded by other "clear" eggs, which are incapable of developing, and Cornevin asks whether we can believe that there is a brusque separation between the two sets, or whether the first at least of the "clear" set may not illustrate this supposed *partial fertilisation.* Romanes also suggested that the supposed effect was due to an absorption by the eggs of surplus sperm-material.

(*c*) Another slightly different suggestion is that the surplus sperms derived from the first sire exert a physiological influence on the *constitution* of the mother, such that subsequent gestations are affected. Perhaps no one will deny that the male may in this way affect the constitution of the female, and Brown-Séquard's experiments on injections of spermine or testicular extract may be recalled in this connection; but it is difficult to conceive that the influence should be of so precise a nature as to

evoke, for instance, the alleged quagga mane and quagga stripes in the second foal of Lord Morton's mare.

Baron compares this supposed influence to the influence of pollen upon fruit (see § 10), and Darwin says that this analogy "strongly supports the belief that the male element acts directly on the reproductive organs of the female" (Darwin, 1868, p. 405). But no specific effect on the female animal has ever been demonstrated.

(*d*) Perhaps the most plausible theory is that the mother is influenced through the fœtus during pregnancy, and that the influence re-acts on subsequent offspring. On this so-called "saturation hypothesis" the suggestion is that the characters of the sire, while expressing themselves in the unborn embryo, also saturate into the dam and affect her constitution in such a precise way that her offspring by subsequent sires may through maternal influence acquire (or inherit ?) some of the characteristics of the first. Thus Sir William Turner (1889), in discussing Lord Morton's case, says, "I believe that the mother had acquired, during her prolonged gestation with the hybrid, the power of transmitting quagga-like characters from it, owing to the interchange of material which had taken place between them in connection with the nutrition of the young one. . . . In this way the germ-plasm of the mother, belonging to ova which had not yet matured, had become modified whilst still lodged in the ovary. This acquired modification had influenced her future offspring, derived from that germ-plasm, so that they in turn, though in a more diluted form, exhibited zebra-like markings."

Similarly, Cornevin (1891) asks, may not the fœtus have in its blood special properties derived from the father, and may not these act like a vaccine on the blood of the mother ? The blood of the mother, thus affected, will act on the ova subsequently fertilised by another sire (Cornevin, 1891, p. 359). So also Harvey, 1851. A similar hypothesis has been suggested to explain

certain facts connected with the so-called transmission of syphilis.

This view did not, however, commend itself to Darwin, for he says (1868, vol. i. p. 405): "It is a most improbable hypothesis that the mere blood of one individual should affect the reproductive organs of another individual in such a manner as to modify the subsequent offspring." He also points out that this hypothesis would not apply to telegony in birds, which has been alleged, though denied by Harvey and still requiring confirmation (Darwin, 1868, vol. i. p. 405).

It is conceivable that something like the "saturation" above indicated may occur in a case of a poison or protective anti-toxin, which might diffuse in and out. We can imagine that a sire infected with some virulent disease, and showing certain structural disturbances associated therewith, may have offspring which are similarly affected, and that the influence from them may pass before their birth into the constitution of the mother, and so affect her that subsequent offspring by a healthy sire are diseased after the manner of the first.

✓Similarly, since it is known that hormones may pass from a mammalian embryo to its mother during the intimate ante-natal symbiosis, it is possible that the constitution of the offspring—partly paternal—might affect the mother's constitution and thus affect a subsequent offspring by another father.

§ 7. *A Statistical Suggestion*

✓ Prof. Karl Pearson (1900, p. 461) has approached the problem from the statistical side. If the female can be influenced at later reproductions by a male who has been associated with her in earlier ones, and if the alleged telegony is not due to some abnormal persistence of the spermatozoa of earlier unions, then in the *permanent* union of a pair we ought to find an increasing influence of the paternal type. But there seems to be, as regards stature, no evidence of any increase in the "hereditary influence"

of the father, therefore "no evidence of any steady telegonic influence."

But an increasing hereditary influence of the same father seems to us rather different from the precise point at issue in the controversy over the occurrence or non-occurrence of telegony. It must be remembered that the bias of the child this way or that depends on the relative potency of the various items in the paternal and maternal contributions to the fertilised egg-cell, and that this relative potency may be affected by a variety of circumstances—*e.g.* the relative age or vigour of the gametes at the time of amphimixis.

Careful comparisons of the families of the same mother by two successive husbands would be interesting—especially if there be anything in the suggestion that the telegonic influence is an influence exerted on the mother during gestation *by the previous offspring*, rather than *directly* through the previous father.

§ 8. *The Widespread Belief in the Occurrence of Telegony*

The belief that offspring sometimes resemble not so much "the father, but an earlier mate of the mother," is widespread among experienced breeders, and, like the belief in the influence of maternal impressions upon the offspring, is probably very ancient. Apart from stock, the belief is often expressed in regard to man himself. "We certainly know that what used to be spoken of as the 'infection of the germ,' but which, following Weismann, we nowadays call 'telegony,' was considered possible by physiologists at the end of the seventeenth century; we know the infection tradition has long influenced Arab breeders, and that believers in this hypothesis may now be found in every part of the world, more especially wherever an overlapping of distinct races occurs—as *e.g.* in the southern states of America and in certain Turkish provinces. Further, until quite recently many biologists considered that what is commonly and conveni-

ently known as Lord Morton's experiment has proved 'infection of the germ' to at least occasionally take place" (Ewart, 1899, p. 57).

It is psychologically interesting, therefore, to ask for some explanation of the widespread belief in the occurrence of a phenomenon the scientific evidence of which seems so slender. There is no doubt, we are told, that the value of a pure-bred bitch at once goes down if she has been accidentally lined by a mongrel, and it is possible that there may be good reason for this apart from the fact that the episode is not one which figures well in the record. It is possible that the constitution of the bitch may be subtly affected by a crossing—especially a fertile crossing—with a dog of inferior strain; and that the deteriorated constitution may react upon future offspring although real telegony does not ensue.

One must remember, however, that the statements one hears are often fairly precise. "If a pointer bitch gets accidentally served by a collie dog and produces a litter, the pups will be of various types, some like the pointer, some like the collie, and some a blend. And let that pointer bitch be afterwards served by a pure pointer dog, the result will be a litter among which the collie type can be unmistakably observed." It is desirable that some effort should be made to secure absolutely definite statements, supplemented by photographs.

It is hardly sufficient to remind ourselves that people are indescribably careless about their beliefs, and that breeders are notoriously superstitious; for considerations of money value have a potent effect in evolving carefulness, and breeding is gradually becoming an art based on scientific conclusions. There must be some basis for the widespread belief, and the answer given by the practical men themselves is that they have had abundant experience of the occurrence of telegony. This assertion leads us to look for phenomena which might be readily mistaken as telegonic, and there can be little doubt that Prof.

Ewart is right in maintaining that the mistake is in the misinterpretation of reversions.

A glance at the chapter on reversion (Chapter V.) will remind the reader that the crossing of different strains often results in apparent "throw-backs." A dark bantam hen paired with an Indian game Dorking produced, amongst others, a cockerel almost identical with a jungle fowl (*Gallus bankiva*)—that is, with the original wild stock. What occurs when different breeds are crossed may occur on a smaller scale when individuals of the same breed, but of different strains, are crossed. When reversionary phenomena occur they usually spell disappointment to the practical breeder. In search of an explanation, he sometimes thinks that he finds one in telegony; that is to say, gives the blame of the reversion not to the immediately preceding crossing, which was theoretically correct, and should have turned out well, but to some remoter, less careful, or perhaps accidental crossing. In this way the remoter sire is made the scapegoat for the reversion, and the belief in telegony has grown.

§ 9. *An Instructive Family History*

A good instance of the way in which cases of alleged telegony evaporate when analysed has been given by Dr. O. vom Rath. It concerns the somewhat intricate family history of certain cats.

A family who had lived for many years in Tunis migrated in 1888 to Baden, taking with them a beautiful pair of kittens. These were none the worse for the change, except that they grew up very unwilling to leave the house, and more or less vicious. The female cat (F) was grey-brown with black stripes; the tom (M) was pitch-black, except a large white spot on the right breast, and had a naturally half-sized left ear. In each litter which they cast there were some abnormal kittens, with rudimentary ear and tail. All these and all the males were destroyed; the normal females were given away. But as the tom (M) became more and more vicious he was castrated, and became peaceful and lazy.

The she-cat (F) was then crossed with an unblemished German tom, but she still produced abnormal kittens in each litter. Thus a strong suggestion of telegony arose.

Further inquiries showed, however, that a normal daughter of F, crossed with a normal German tom, had borne a red male with rudimentary left ear and rudimentary tail. Inquiries as to the pedigree of F and M showed that *f*, the mother of F, had a rudimentary tail, but no rudimentary ear, and was like F in colour. This *f* had been crossed with a red tom (R), who had a rudimentary ear and tail; there was but one litter, which was destroyed, and R soon afterwards died. Then *f* was paired with a normal black younger brother (S) of the deceased (R). From this normal S and from this *f* with a rudimentary tail, F sprang. But the two parents of *f* and the two parents of R and S were relatives, belonging to a family in which a rudimentary ear and tail were common—all springing from a pair which the owner of F and M had found in a hollow tree near Tunis.

Dr. vom Rath has more to tell, but enough has been quoted to show the correctness of his conclusion that there was no telegony at all. There was a strong family tendency to having a rudimentary ear and tail. But it is evident that if Vom Rath had not had patience to search out the family history, the case for the occurrence of telegony would have been fairly good—at least as good as many others.

§ 10. *A Note on Xenia*

The mysterious name "xenia," which seems to mean "guest-gifts," was applied by the botanist Focke to cases where the pollen from the "male" parent seemed to affect the tissue of the maternal ovary—the substance of the seed, or even the fruit, as distinguished from the embryo itself.

Correns has made careful experiments with maize and estab-

lished that there at least xenia occurs. When the white-grained variety (*Zea alba*) is pollinated from the blue-grained variety (*Zea cyanea*), the majority of the seeds have white endosperm around the embryo, but a few have blue endosperm. The converse is likewise the case. It must be noted that the effect is only on the so-called "endosperm," or nutritive layer around the embryo; the envelope of the seed, for instance, is never affected.

What happens seems to be this. The pollen-tube arising from the pollen-grain contains *two* generative nuclei, which arise by the division of one. Of these two nuclei, one fertilises the egg-cell, the other fuses with what are called the polar-nuclei (a fact discovered by Nawaschin and Guignard). Thus there is a sort of double fertilisation within the embryo-sac; the one results in the embryo, the other gives origin to the endosperm.

Thus we see that xenia (in the well-authenticated case of maize) is no mysterious influencing of maternal tissue by the pollen-tube, and that it does not require Darwin's hypothesis of a migration of "gemmules" from the fertilised ovum into the surrounding tissue. It is a phenomenon *sui generis*, due to the very peculiar "double fertilisation." As Weismann points out, it corroborates the view that the nuclei are the vehicles of the hereditary qualities.

Many of the alleged cases of xenia are cited in Prof. Delage's great work (1903, p. 252), the most picturesque being that of an apple-tree of Saint Valery. "This tree was sterile through the abortion of its stamens. Every year the young girls gathered branches from other apple-trees in flower, and shook them over the flowers of the non-staminate tree to fertilise them. Tillet De Clermont-Tonnerre (1825) relates that the resulting fruits recalled in their size, colour, and taste, those of the trees which had furnished the pollen."

It is to be feared, however, that many of the alleged cases of xenia will not stand examination. Thus the records in regard

to peas do not seem to be relevant, since the two halves of the pea-seed are of course the cotyledons and part of the embryo. Some of the phenomena seem simply ordinary cases of Mendelian inheritance (see Chapter X.).

Some of the cases where it is said that the whole fruit is affected —*e.g.* in grapes and oranges—well deserve further investigation.

§ 11. *Maternal Impressions*

It is a time-honoured belief that the mental states—especially vivid sense-impressions and strong emotions—of a pregnant mother may so affect the unborn offspring that structural changes result which have some correspondence with the maternal experience. The belief was hardly doubted till Blondel began to criticise it early in the eighteenth century.

Every one allows that the mother's health in the widest sense may react on the offspring, within what limits we hardly know; but it is a very different matter to believe in definite and specific structural effects. There can be no doubt that the firmly rooted theory is in the main quite unscientific, except in the sense that it expresses the instinct to discover some cause for peculiar phenomena. A child has hypertrichosis: did not the mother look too long at a picture of John the Baptist in a hairy robe? A white mother has a dark child: what can she say but that she was frightened by a Moor?

The abundant literature on the subject has been carefully studied by Dr. J. W. Ballantyne, and it need hardly be said that his general verdict is wholly against the tenability of the theory, except in a very refined form.

The mental experiences of the mother have been held to explain peculiarities of colour, abnormal hairiness, birth-marks, malformations, and even conception itself. The *post hoc ergo propter hoc* argument has never been more wildly used, and the result has been a retardation of the study of ante-natal pathology.

Jacob's trick of using peeled wands to influence the colour of

his stock is still practised in modified form. A famous breeder of cattle has assured me that to obtain a particular colour of calf from a cow which persistently refused to produce what he wanted, he followed the patriarch's prescription with success. He had her covered blindfold; after the sire had gone he brought to her a heifer of the desired colour, and that was the first object she saw when the bandages were removed; she was left with the heifer as a companion to occupy her mind, and the result in due time was a calf of the desired colour. Nor was this an isolated case.

What can one say—the credibility of the witness being secure—except the unsatisfactory word "coincidence"? One requires to know in what direction, as regards colour, the sire was prepotent. One requires to know how many failures are forgotten in proportion to the successes remembered?

It is admitted that shock and distress and the like may have prejudicial effects on the unborn offspring. It is stated that after the Irish famine and after the siege of Paris there were many children born with stigmata of various sorts, and these were sometimes referred back to particular experiences instead of to the general state of malnutrition and nervous exhaustion. But to associate a particular structural defect with a particular mental impression seems an untenable position. The *modus operandi* is difficult to conceive of. Sometimes, indeed, the maternal-impression theory is demonstrably untenable, when the impression occurs late in pregnancy, for most of the great events in development occur very early. We have also to remember the multitude of cases in which, in spite of very startling maternal experiences, the offspring is quite normal. In comparison with this multitude of cases where nothing happens, the number of really puzzling cases is very small, and may be dismissed as coincidences.

At the same time it is always unwise to speak of impossibilities in regard to matters which are inadequately known and imperfectly understood. That we cannot imagine the nature of a

physiological nexus does not prove its non-existence. Thus, as in regard to the transmission of acquired characters and telegony, we may be scientifically sceptical and give a verdict "non-proven," without dogmatically saying "impossible."

We can understand how contact with a puzzling case gives the observer pause. A medical practitioner of keen scientific intelligence told me of a patient who, during pregnancy, had seen her husband suffer a serious accident. His arm was cut open by a falling block. As the impression seemed to weigh on the woman's mind in its relation to the unborn child, the doctor was asked to reassure her—which he did, with confidence and no doubt with skill. He was rather startled, however, when the time came, to find that the child he ushered into the world *had* a mark on the arm suggestive of the father's wound, and on the same arm.

We must remember that for a prolonged period the unborn child is part and parcel of the mother—almost an integral part of herself—and we are beginning to know enough of the influence of mind upon body to make us cautious in dogmatising as to the possibilities of what Ballantyne * finely calls "the mysterious wireless telegraphy of ante-natal life."

* While expressing his disbelief in the potency of maternal impressions to cause conditions in the fœtus resembling the impression, Dr. J. W. Ballantyne cautiously adds ("Discussion on Heredity in Disease," *Scottish Med. and Surg. Journ.* vi. 1900, p. 310) that "to whatever extent we believe the mind capable of influencing the state of a part of the body, to that same extent, or to a degree rather less, the mother's mind might influence her parasitic growth—*i.e.* the fœtus *in utero*. But this amount of belief would of course vary very much in accordance with the elasticity of our belief regarding the influence of the mind over the body."

CHAPTER VII

THE TRANSMISSION OF ACQUIRED CHARACTERS

"A right answer to the question whether acquired characters are or are not inherited underlies right beliefs, not only in Biology and Psychology, but also in Education, Ethics, and Politics."

HERBERT SPENCER.

§ 1. *Importance of the Question.*
§ 2. *Historical Note.*
§ 3. *Definition of the Problem.*
§ 4. *Many Misunderstandings as to the Question at Issue.*
§ 5. *Various Degrees in which Parental Modifications might affect the Offspring.*
§ 6. *Widespread Opinion in favour of Affirmative Answer.*
§ 7. *General Argument against the Transmissibility of Modifications.*
§ 8. *General Argument for the Transmissibility of Modifications.*
§ 9. *Particular Evidences in support of the Affirmative Answer.*
§ 10. *As regards Mutilations and the Like.*
§ 11. *Brown-Séquard's Experiments on Guinea-pigs.*
§ 12. *Negative Evidence in favour of the Affirmative Answer.*
§ 13. *The Logical Position of the Argument.*
§ 14. *Indirect Importance of Modifications.*
§ 15. *Practical Considerations.*

§ 1. *Importance of the Question*

No one is at present entitled to rank the transmission of "acquired characters"—*i.e.* somatic modifications—among *the facts of inheritance*, and the logical place for a discussion of this subject should be beside other disputed questions, like the occurrence or non-occurrence of telegony. But we have given special prominence to a discussion of this problem because of its great importance both practically and theoretically, and because of the abundant debate which has been aroused over it.

Not a Merely Academic Problem.—The question as to the transmissibility of characters acquired during life by the body of the parent as the result of changes in environmental or functional influences is much more than a technical problem for biologists. Our decision in regard to it affects not only our whole theory of organic evolution, but even our every-day conduct. The question should be of interest to the parent, the physician, the teacher, the moralist, and the social reformer—in short, to us all.

If the particular results of changes or peculiarities in individual nurture, education, and experience do *not* directly and specifically affect the inherited nature of the offspring, there must be a revision of some current psychological and pedagogical opinions; but it must be borne in mind that man's rich *external heritage* of tradition and convention, custom and institution, law and literature, art and science, makes his case quite peculiar, for the results of man's external heritage are often such as might have come about if acquired characters *were* heritable.

If the particular results of changes or peculiarities in individual "nurture" do not directly and specifically affect the inherited nature of the offspring, there must be a revision of that theory of organic evolution which is usually called Lamarckian, in which it is a central postulate that whatever is acquired may also be transmitted.

Spencer's Estimate of the Importance of this Question.—After contrasting the two hypotheses of the transmissibility and the non-transmissibility of acquired characters, Herbert Spencer said: " Considering the width and depth of the effects which the acceptance or non-acceptance of one or the other of these hypotheses must have on our views of life, the question, Which of them is true? demands beyond all other questions whatever the attention of scientific men. A grave responsibility rests on biologists in respect of the general question, since wrong answers lead, among other effects, to wrong belief about social affairs and to disastrous social actions." This authoritative statement removes all need of apology for the prominence which we have given to the question.

An Interminable Question.—The attention of scientific men which Herbert Spencer demanded for this problem has not been grudgingly given. The subject has been keenly debated for many years; there are, as our bibliography will show, scores of papers and not a few books devoted to its discussion. Indeed, one of the most tolerant of biologists, Prof. W. K. Brooks, has spoken of it as " the interminable question." Those who give the affirmative answer have not succeeded in proving their case; as for the other side, how can they prove a negative? Therefore, while we have no hesitation as to the verdict of " non-proven " to which the evidence *at present available* points, we do not expect a satisfactory issue until many years of experimental work have supervened.

Why, then, if a satisfactory termination be not at present possible, and if no unanimity even among experts can be looked for, should we enter upon the discussion once more? Prof. Brooks states our warrant in a quotation from Berkeley's *Siris*: " It is Plato's remark in his *Theætetus*, that while we sit still we are never the wiser, but going into the river and moving up and down is the way to discover its depths and shallows. If we exercise and bestir ourselves we may even here discover something."

Experiment is doubtless most urgent, but misunderstandings in regard to the problem are still so prevalent that we take courage in attempting a re-discussion, from which we have tried to eliminate obscurity and prejudice.

§ 2. *Historical Note*

Doubt as to the transmission of acquired characters is certainly not novel, though Galton and Weismann deserve credit for defining the scepticism.

Brock has pointed out that the editor, whoever he was, of Aristotle's *Historia Animalium* seems to have differed from his master on this subject. Aristotle had referred to the transmission of the exact shape of a cautery mark, but the editor insinuated a doubt as to credibility of instances of this sort.

Kant.—In modern times Kant was one of the first to express a firm disbelief in the transmission of individual peculiarities; Blumenbach inclined to the same opinion; but neither seems to have defined precisely what he intended to exclude from the bundle of inheritance.

Prichard.—James Cowles Prichard (b. 1786), a well-known anthropologist, anticipated as early as 1826 some of the characteristically modern views on evolution. His importance has been pointed out by Prof. Edward B. Poulton. In the second edition of his *Researches into the Physical History of Mankind* (1826), Prichard stated the case in favour of the general evolutionist interpretation of animate nature, recognised the operation of natural and artificial selection, and not only drew a clear distinction between acquired and inborn peculiarities, but argued that the former were not transmitted. He was not rigidly consistent, however, and his convictions seem to have weakened in after years; yet his anticipation of one of Weismann's positions by more than half a century is very interesting.

In more recent times we find sporadic expressions of scepticism

as to the transmission of acquired characters—*e.g.* by the morphologist His and the physiologist Pflüger; but, as we have said, the focussing of the question was due to Galton and Weismann.

Galton.—Thus Galton in 1875 stated his opinion that the current theory of the inheritance of characters acquired during the lifetime of the parents " includes much questionable evidence, usually difficult of verification. We might almost reserve our belief that the structural cells can react on the sexual elements at all, and we may be confident that at the most they do so in a very faint degree—in other words, that acquired modifications are barely, if at all, *inherited* in the correct sense of that word."

Galton's position at that time may be summed up as follows:

(1) In regard to climatic variations, Galton doubted the reality of any reaction of the " body " upon the germs, but believed that the germs are themselves *directly* affected.

(2) The same is true in regard to many diseases that have been acquired by long-continued irregular habits.

(3) The cases of the *apparent* inheritance of mutilations are outnumbered by the overpowering negative evidence of their non-inheritance.

(4) It is hard to find evidence of the power of the personal structure to react upon sexual elements that is not open to serious objection. That which appears the most trustworthy lies almost wholly in the direction of nerve changes, as shown by the inherited habits of tameness, pointing in dogs, and the results of Dr. Brown-Séquard's experiments on guinea-pigs.

Weismann.—But Weismann gave the scepticism an even sharper point. He denied *all* transmission of acquired modifications, partly because he found the evidence so flimsy and anecdotal, partly because he could not conceive of any mechanism whereby the transmission of a particular acquired modification could be effected, and partly because his whole theory of heredity and variation raised strong probabilities against the view that

acquired characters were transmitted. On Weismann's view the sole fountain of specific change is in the germ-plasm of the sex-cells. It is true that the environment makes dints on the organism, but only upon its *body*; the reproductive cells, through which alone the change could be transmitted, are either unaffected or are not affected in such a definite way as to bring about the transmission of the parental modification. It is true that the results of changed function (use and disuse) are often very marked, and very important *for the individual;* but they are not transmitted as such or in any representative degree, and therefore are of no direct account in the evolution of the species. Thus the ground is taken from under the feet of Buffonians and Lamarckians, and the whole burden of organic progress is laid upon germinal variation and the processes of selection.

The following sentences indicate Weismann's original position:

(1) "Acquired characters are those which result from external influence upon the organism, in contrast to such as spring from the constitution of the germ."

(2) "Characters can only be inherited in so far as their rudiments ('Anlagen') are already given in the germ-plasm."

(3) "Modifications which are wrought upon the formed body, in consequence of external influences, must remain limited to the organism in which they arose."

(4) "So must it be with mutilations, and with the results of use or disuse of parts of the body."

(5) "No such modifications of the soma (affected by environment or by use and disuse) can be transmitted to the germ-cells, from which the next generation springs. They are, therefore, of no account in the transformation of the species."

(6) "The only principle that remains for the explanation of the transformation of the species is direct germinal variation."

On germinal variations natural selection operates in the usual way. The helpful subsidiary theory of germinal selection was afterwards suggested, and various saving clauses were added, which do not, however, affect the clearness and strength of Weismann's original position.

Lamarck's Laws.—It may be fairly said that the *fons et origo* of the affirmative position was Lamarck. Though he did not originate, he formulated and illustrated the theory of the inheritance of acquired characters. He maintained the transmissibility of modifications due to increased and decreased and changed use, and also of modifications due to environmental change, whether directly induced, or indirectly induced by altered function. The giraffe has attained its long neck by stretching it for many generations; swimming birds have got webbed feet because they stretched their toes in the water; wading birds have got long legs because they stretched them; the mole has very small eyes because it has ceased to use them; the whalebone whale has no functional teeth because it has acquired the habit of swallowing its food without mastication; and so on.

Lamarck's two laws of nature, which he said no observer could fail to confirm, were: *

(1) In every animal that has not passed beyond the term of its development, the frequent and sustained use of any organ strengthens it, develops it, increases its size, and gives it strength proportionate to the length of time of its employment. On the other hand, the continued lack of use of the same organ sensibly weakens it; it deteriorates, and its faculties diminish progressively, until at last it disappears.

(2) Nature preserves everything that she has caused the individual to acquire or to lose by the influence of the circumstances to which the race has been for a long time exposed, and consequently by the influence of the predominant use of certain organs (or in consequence of their continued disuse). She does this by the generation of new individuals, which are produced with the newly acquired organs. This occurs, provided that the acquired changes were common to the two sexes, or to the individuals that produced the new forms.

Prof. E. Ray Lankester has pointed out (1894) that Lamarck's

* I have taken the translation from T. H. Morgan's *Evolution and Adaptation* (1903), p. 226.

first and second laws are contradictory the one of the other. In correspondence with the normal conditions of the environment, organisms show "responsive" quantities in their parts; but change a young organism to an environment quantitatively different, and it shows *new* responsive quantities in the parts of its structure concerned, new or *acquired* characters.

"So far, so good. What Lamarck next asks us to accept, as his 'second law,' seems not only to lack the support of experimental proof, but to be inconsistent with what has just preceded it. The new character, which is *ex hypothesi*, as was the old character (length, breadth, weight of a part) which it has replaced—a response to environment, a particular moulding or manipulation by incident forces of the potential congenital quality of the race—is, according to Lamarck, all of a sudden raised to extraordinary powers." It is declared to be transmissible, that is, it alters the potential character of the species, so as to persist when other quantitative external conditions are substituted for those which originally determined it. But this has never been experimentally proved, and there is strong reason for holding it to be improbable.

"Since the old character (length, breadth, weight) had not become fixed and congenital after many thousands of successive generations of individuals had developed it in response to environment, but gave place to a new character when new conditions operated on an individual (Lamarck's first law), why should we suppose that the new character is likely to become fixed after a much shorter time of responsive existence, or to escape the operation of the first law? Clearly there is no reason (so far as Lamarck's statement goes) for any such supposition, and the two so-called laws of Lamarck are at variance with one another.

"In its most condensed form my argument has been stated thus by Prof. Poulton (*Nature*, vol. li., 1894, p. 127); Lamarck's 'first law assumes that a past history of indefinite duration

is powerless to create a bias by which the present can be controlled; while the second assumes that the brief history of the present can readily raise a bias to control the future.'" (See E. Ray Lankester's *Kingdom of Man*, 1907, pp. 128–130.)

Lamarckism remains alive.—The Lamarckian position is still stoutly maintained—usually in more or less modified form—by many prominent naturalists, especially in France and America. It is often held along with a more or less half-hearted Darwinism, just as Darwin combined some Lamarckism with his own selectionist doctrine—even in spite of his protest, "Heaven forfend me from Lamarck nonsense of a tendency to progression, adaptations from the slow willing of animals, etc." Though Alfred Russel Wallace has said, "The hypothesis of Lamarck has been repeatedly and easily refuted by all writers on the subject"; though Huxley said, "The Lamarckian hypothesis has long since been justly condemned"; though Ray Lankester has said that perhaps the greatest step of progress in modern ætiology will be the complete removal of all taint of Lamarckism,—there remains a vigorous school of Lamarckians and a still more vigorous school of Neo-Lamarckians, who, whatever be the truth in regard to the transmission of acquired characters, have got a firm grip of the often-overlooked commonplace that *the organism is an active, self-assertive, self-adaptive living creature—to some extent master of its fate.*

§ 3. *Definition of the Problem*

A Protest.—Much time and energy have been wasted on the discussion as to the transmissibility or non-transmissibility of "acquired characters" or somatic modifications, through lack of precise definition of the terms. Usually, though not always, the fault has been with the supporters of the affirmative position, who have failed to observe the rules of the game by ignoring the definitions of those who find themselves forced to a negative

conclusion. By all means let there be a critical discussion as to the best definition of "an acquired character," "a modification," "a somatic change induced on the body by environmental or functional influences"; by all means let there be a criticism of terms and categories—the minting of a perfectly unambiguous word for somatic modifications would be most welcome: but if the sheaves of facts and alleged facts are to be thrashed out with the end of getting at the wheat of truth, we *must* adhere to certain definitions—notably, of course, to those given by Weismann, who brought the problem in its modern aspect into focus. Even a sense of humour should hinder a young medical practitioner from thinking that he makes for progress by advancing an argument which has no cogency unless the biological dictionary be first re-edited. It should be evident that a discussion over which some of the wisest heads in Europe and America have pondered cannot be, as some have had the effrontery to declare it, a mere play of words. Is it too much to ask of those who are keen to break a lance with the Biologist of Freiburg that they should first at least read *The Germ-Plasm*?

What is an Acquired Character?—In our previous discussion of "heredity and variation" we have briefly expounded the distinction between germinal, blastogenic, constitutional, endogenous "variations," and bodily, somatogenic, acquired, exogenous "modifications." An acquired character, or a somatic modification, may be defined as a structural change in the body of a multicellular organism, involving a deviation from the normal, directly induced during the individual lifetime by a change in environment or in function (use and disuse), and such that it transcends the limits of organic elasticity, and therefore persists after the factors inducing it have ceased to operate.

Illustrations.—Dwarfing of Japanese trees, deformation of trees by the wind, blanching of plants grown in darkness, changes directly induced by transplantation, persistent sun-burning, change

of colour after particular diet, callosities induced on the skin by pressure, *e.g.* those at first produced on the finger-tips of one who is learning to play the violin, dwarfing of animals in confined space, increased muscular development by exercise, atrophy of muscles through disuse, chronic fatigue of nerve-cells, alterations in the walls of the food-canal through particular diet, changes in the skeleton as the result of specialised activities, increased growth of hair, etc., after importation to a warm climate, accumulation of fat as the result of modified nutrition, and so on through a long list.

To understand the question clearly we must spend a little time and thought over it. Let us briefly consider the various relations between an organism and its surroundings.

1. **Relation of Dependence between Organism and Environment.**—It is a familiar fact that a living creature is dependent upon its surroundings. A great part of life consists in action and reaction between the organism and its environment. It is a profound commonplace that between the animate system—so incomprehensibly unified—and its inanimate milieu, there is a continual coming and going of matter and energy. On this life depends. The may-fly during its short aerial life must breathe even if it does not feed; the philosopher requires his dinner, just as his dog does. This may be called the relation of constant and normal environmental dependence—necessary to the development and to the continuance of the organism.

2. **Transient Adjustments.**—But surroundings are changeful, and the living creature changes with them. A great part of life consists of *effective responses* to external changes; consciously or sub-consciously the organism adjusts itself to changes in its environment, or works in the direction of adjustment. There is bright sunshine and our pulse beats more quickly; the external temperature rises and we perspire. Thousands of these changes are familiar, saving life from monotony. Yet in regard to many there remains no abiding result that can be detected. There are structural changes attendant on normal nerve-fatigue, but in rest and food we gain almost complete recuperation. No

doubt there is always *some* lasting impression, for even the bar of iron is never quite the same after it has been once struck; but the results of the slight organic changes we have been alluding to are usually lost as the sand-ripples are lost when the tide turns. They are the merely transient results of responses to frequently recurring environmental changes to which the organism is well accustomed.

3. **Adjustments which persist for a Considerable Time.**—Insensibly, however—for it is all a matter of degree—we pass from transient results to others which last for a considerable time. We are browned by the sun on our summer holiday, and the result may last far into the autumn. The change, though still very superficial, has taken a firmer hold. The world is full of illustrations—the increase in the child's weight after a month at the farm, the increase in the size of the muscles after a course of Sandow exercises, the warping of the plant-stem which has been illumined from one side only, the blanching of the banked-up celery. But these results do not last long after the inducing conditions have ceased to operate. Sooner or later there is a return to the normal. Like a bow unstrung, the organism rebounds approximately to its previous state. The stimulus ceases or the absent stimulus is restored, and the organism, as if at the command "As you were," returns to the *status quo*.

4. **Modifications.**—Insensibly, however—for it is still only a matter of degree—we pass from these temporary changes to others which are demonstrably permanent. For there are cases where the new stimulus provokes a structural change, which persists after the stimulus has ceased. As we have put it, metaphorically, the limit of organic elasticity has been transcended. These are what in technical language we call "acquired characters" or "modifications."

The Englishman who works half his lifetime under a tropical sun may become so tanned that the result does not disappear

during all the years in which he enjoys his pension at home. He has changed his skin, but he cannot by any means change it back again. Through prolonged disuse from early years a muscle may pass into a state of atrophy, and may so remain throughout life. Pressure on the little toe may so deform it, that even in the "easiest" shoes it can never right itself. A tree may be blown out of shape by the wind, and the crooked bough may never be straightened. Over-exertion may strain the heart permanently. A sudden shock may be followed by a whitening of the hair from which there is no natural recovery.

5. **Modifications and Variations.**—When we analyse *the observed differences* between fellow members of a species, we find that some of them can be definitely associated with peculiarities of function and environment. They can be more or less accounted for physiologically in terms of some change in surrounding influences or of some change in function thereby induced. They may not be hinted at in the young forms, but they begin to appear when the peculiar conditions begin to operate, and they are usually exhibited in some degree by all organisms of the same kind which are subjected to the same change of conditions. Furthermore, they can be experimentally brought about. These are "modifications."

By those who measure observed differences they are usually slumped along with true variations, but this appears to us to lead to confusion. *True variations are those peculiarities which remain when all the modifications are subtracted from the total of observed differences.*

It goes without saying that the distinction cannot *always* be drawn in practice. Often, however, it is quite apparent, and in any case the theoretical distinction is clear. Variations, in the strict sense, cannot be causally related to peculiarities in habit or surroundings; they are often hinted at in the earliest stages—even before birth; and they are very unequal even

among organisms whose conditions of life seem absolutely identical. We refer them to changes in the germinal material before or during fertilisation. We call them endogenous, constitutional, blastogenic; and there is no doubt that they are transmissible, though they are not always transmitted.

Is there really an Antithesis?—Some subtle minds have found satisfaction in maintaining that the distinction between an acquired modification and an inborn variation is a distinction without a difference. In his interesting *Problems of Biology* Mr. George Sandeman points out that every acquired quality is germinal (*i.e.* there are in the organisation the rudimental possibilities of it), and that every germinal quality is also acquired (*i.e.* it requires to be nurtured by appropriate conditions if it is to develop). In this epigram there is undoubtedly truth, but is it relevant?

No doubt the possibility of the modification must be in the organism, just as the possibility of an explosion is in the barrel of gunpowder. The environment is not creative; yet, as a matter of fact, it seems possible to distinguish between the actual modification which we see and measure and the possibility of it which we presuppose.

Similarly, it is very true that the potentialities so marvellously embodied in the fertilised egg-cell require appropriate environing conditions if they are to be realised, for, as His observed long ago, "it is a piece of unscientific mysticism to suppose that heredity will build up an organism without mechanical means."

The common jelly-fish (*Aurelia aurita*) often has a pentamerous instead of a tetramerous symmetry. This is a variation of germinal, endogenous origin. Of course it requires an environment to develop in, but we cannot causally relate the structural peculiarity to any peculiarity in the environment. It seems to be logically quite distinguishable from a modification.

Discussing words is often indescribably tiresome, but it is better than misunderstanding them. "Inheritance of acquired characters"

may be a most unfortunate phrase, but it has come to have a perfectly definite technical meaning and usage, which any normal person can understand in a few minutes. Prof. W. K. Brooks, in his *Foundations of Zoology*, says that he never uses the phrase "inheritance of acquired characters" except under protest, and this may be commendable restraint; but it seems to us inconsistent with his usual wisdom to go on to say, "If any assert that the dog inherits anything which his ancestors did not acquire, their words seem meaningless; for, as we use words, everything which has not existed from the beginning must have been acquired—although one may admit this without admitting that the nature of a dog is, wholly or to any practical degree, the inherited effect of the environment of his ancestors." But as the word "acquired" is now a technical term, meaning wrought out on the body as the result of changes in environmental or functional stimuli, we fail to see that, as we use the words, there is anything meaningless in the first assertion, or any warrant for the second.

Summary.—What forms the material basis of all inheritance, in all ordinary cases of sexual reproduction among multicellular organisms, is the fertilised ovum. The question under discussion is, physiologically stated, whether we can conceive that structural changes in the body of a parent, induced by changes in functional or environmental influence, can so specifically affect the reproductive cells that these will, if they develop, reproduce in any degree the modification acquired by the parent or parents. The question under discussion, logically stated, is whether there are any secure phenomena of inheritance which forcibly suggest the reality of the transmission of acquired characters; or whether, if such phenomena there be, a simpler interpretation may not be found. If, summing up in Galton's phrase, we call environmental and functional influences "nurture," our question is seen to be the exceedingly important one, May the bodily results of peculiarities in parental "nurture" be as such transmitted, or is it the germinal "nature" alone that constitutes the inheritance?

§ 4. *Many Misunderstandings as to the Question at Issue*

The precise question is this : *Can a structural change in the body, induced by some change in use or disuse, or by a change in surrounding influence, affect the germ-cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in a slight degree, the modification which the parent acquired ?*

Before we pass to discuss the evidence pro and con it will be useful to notice some frequently recurring *misunderstandings*, the persistence of which would make further argument futile.

Misunderstanding I—*How can there be progressive evolution if acquired characters are not transmitted ?*—Those who have not thought clearly on the subject often shake their heads sagely and remark that they "do not see how evolution could have been possible at all unless what is acquired by one generation is handed on to the next." To this we have simply to answer (1) that our first business is to find out the facts of the case, careless whether it makes our interpretation of the history of life more or less difficult, and (2) that in the supply of germinal *variations*, whose transmissibility is unquestioned, there is ample raw material for evolution. We know a little about the abundant crop of variations at present supplied; there is no reason to believe that it was less abundant in the past.

Misunderstanding II—*Interpretations are not facts.*—There are many adaptive characters in plants and animals which may be superficially interpreted as due to the direct result of use and disuse or of environmental influence. The Lamarckians have so interpreted them, and the Lamarckian way of looking at adaptations has become habitual to many uncritical minds. They see on modern flowers the footprints of insects which have visited them for untold ages ; they speak of the dwindling of the whale's hind-limbs through disuse, of

the hardening of the ancestral horses' hoofs as they left the marshes and ran on harder ground; they picture the giraffe by persistent effort lengthening out its neck a few millimetres every century, as the acacia raised its leaves higher and higher off the ground; and they say that animate nature is so full of evidences of the inheritance of acquired characters that no further argument is needed.

But all this is a begging of the question. It is easy to find structural features which *may be interpreted* as entailed acquired characters, *if* acquired characters can be entailed. Obviously, however, we must deal with what we can prove to be modifications, or with what we can plausibly regard as modifications because we find their analogues in actual process of being effected to-day.

It is easy to say that the blackness of the negro's skin was produced by the tropical sun, and that it is now part of his natural inheritance. It is easy to say this, but absolutely futile. Let us first catch our modifications.

The Golden Rod (*Solidago virgaurea*) growing on the Alps is precocious in its flowering when compared with representatives of the same species growing in the lowlands. Hoffmann found that Alpine forms transplanted to Giessen remained precocious, therefore the acquired precocity had become heritable. But there is no evidence that the precocity *was* acquired; it may have been the outcome of the selection of germinal variations.

The African Wart-hog (*Phacochœrus*) has the peculiar habit of kneeling down on its fore-limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind-limbs. It has strong horny callosities protecting the surfaces on which it kneels, and these are seen even in the embryos. This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character. It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection.

Misunderstanding III—*Begging the question by starting with what is not proved to be a modification.*—There is no relevancy in citing cases where an abnormal bodily peculiarity re-appears generation after generation, unless it be shown that the peculiarity *is* a modification, and not an inborn variation whose transmissibility is admitted by all. Short-sightedness may recur in a family-series generation after generation, but there is no evidence to prove that the original short-sightedness was a modification. In all probability, short-sightedness is in its origin a germinal variation, like so many other bodily idiosyncrasies.

In regard to some diseases, such as rheumatism, it is often said dogmatically by those who know little about the matter that the original affection in the ancestor was brought about by some definite external influence—such as a cold drive or a damp bed; but it seems practically certain that in all such cases we have to do with an inborn predisposition, to the expression of which the cold drive or the damp bed was merely the liberating stimulus, comparable to the pulling of the trigger in a loaded gun. The liberating stimulus is, of course, of great importance, both in the case of the gun's discharge and the organism's disease, but it only goes a little way towards a satisfactory interpretation in either case. Not that we can explain the origin of rheumatism or shortsightedness or any such thing—there is no explanation in calling them germinal variations that cropped up; but we are almost certain that they never are modifications or acquired characters.

Herbert Spencer twits those who are sceptical as to the transmission of acquired modifications with assigning the most flimsy reasons for rejecting a conclusion they are averse to; but when Spencer cites the prevalence of short-sightedness among the "notoriously studious" Germans, the inheritance of musical talent, and the inheritance of a liability to consumption, as evidence of the inheritance of modifications, we are reminded of the pot calling the kettle black.

Over and over again in the prolific literature of this discussion the syllogism is advanced, either in regard to gout or something analogous—

> Gout is a modification of the body, an acquired character;
> Gout is transmissible;
> Modifications are sometimes transmissible.

It may be formally a good argument, but there is every reason to deny the major premiss. There is no proof that the gouty habit had an exogenous origin—that it was, to begin with, for instance, the direct result of high living; though it is generally admitted that excesses in eating or drinking may give a stimulus to its expression. "The conclusion I have arrived at," says Prof. D. J. Hamilton (1900, p. 297), "is that the gouty habit of body has arisen as a variation, and as such is hereditarily transmissible, and that excess of diet and alcohol merely renders the habit of body apparent." It may also be pointed out that gout and rheumatism and the like are rather *processes of metabolism* than structural modifications, though the latter may ensue.

After pointing out the irrelevancy of citing cases of the hereditary recurrence of polydactylism, hæmophilia, colour-blindness in man, or the absence of horns in cattle or of tails in cats, as instances of the transmission of acquired characters, Prof. Ernst Ziegler says (1886, p. 13): "Only that can be regarded as 'acquired' which is produced in the course of the individual life, during or after the period of development, exclusively under the influence of external conditions; the term is in no wise applicable to peculiarities which, as one says, arise of themselves from a predisposition already present in the germ."

Let us state the case once more. There is no doubt that the expression of a germinal variation during the lifetime of an individual may be sometimes definitely associated with a particular external stimulus. It may thus be mistaken for a modification, and mistakenly spoken of as "acquired." But the relation between the

provoking stimulus and the expression of the innate tendency or predisposition is more or less arbitrary—various kinds of stimuli will have the same result; whereas the relation between an environmental influence and the induced modification is more or less constant—similar influences having similar results—and is more strictly causal. An external stimulus may provoke the expression of a germinal variation, as when a mouse provokes hysteria; but this is different physiologically from what occurs when the sun produces sun-burning.

A certain abnormal psychosis, which may not have been hinted at during early years, suddenly emerges under provocation. It is carelessly spoken of (even in the law courts) as due to that provocation—a fright, a wound, a debauch, a railway accident, a night's exposure, and so on, and it is carelessly thought of as "acquired"; it is recovered from, but it re-appears in the offspring: *therefore* an acquired character may be transmitted. But there is the strongest probability that what was called an acquired psychosis was primarily germinal, and might have emerged under quite different stimulation—for instance, under the normal events of puberty and parturition.

Another version of this misunderstanding is seen in references to the improvement of a breed in the course of generations, as the result, it is supposed, of functional modifications. Practice makes perfect in the individual, therefore also in the race. But we have seen no cases cited where the results were not hopelessly complicated by the occurrence of selection and elimination, which, by acting on constitutional variations, may quite well account for what is hastily referred to modification-inheritance.

Herbert Spencer was keenly aware of the misunderstanding which we have been discussing. "Such specialities of structure as are due to specialities of function are usually entangled with specialities which are, or may be, due to selection, natural or artificial. In most cases it is impossible to say that a structural peculiarity which seems to have arisen in offspring from a functional peculiarity in a parent is wholly independent of some congenital peculiarity of structure in the parent, whence this functional peculiarity arose. We are restricted to cases with which natural or artificial selection can have had nothing to do, and such cases are difficult to find."

Yet it is strange that he should point to such facts as the following: the bones of the wing in the domestic duck weigh less and the bones

of the leg more in proportion to the whole skeleton than do the same bones in the wild duck ; in cows and goats which are habitually milked the udders are large ; moles and many cave-animals have rudimentary eyes. Cases like these may be in part regarded as instances of individually re-acquired modifications, but they are for the most part readily interpreted as due to the selection of germinal variations.

Misunderstanding IV—*Mistaking the reappearance of a modification for transmission of a modification.*—It is of little service to cite cases where a particular modification reappears generation after generation unless it be shown that the change recurs *as part of the inheritance*, and not simply because the external conditions which evoked it in the first generation still persisted to evoke it in those that followed. Reappearance is not synonymous with inheritance.

Illustration.—When Prof. Nägeli brought Alpine plants (*Hieracium*, etc.) to the Botanical Garden at Munich, many became in the first year so much changed that they were hardly recognisable as the same species, and their descendants in the garden were likewise quite different from their Alpine ancestors. The small Alpine hawkweeds became large and thickly branching, and blossomed freely. In some cases many generations were observed—even for thirteen years ; there was no doubt as to the *reappearance* of the acquired characters ; but it was not thereby proved that the reappearance was due to the inheritance. On the contrary, that the reappearance was due to the persistence of the novel conditions, to the changes which these directly impressed on each successive crop, was shown by the fact that when the plants were removed to poor, gravelly soil, the acquired characters disappeared, and the plants were re-transformed into their original Alpine character. " The re-transformation was always complete, even when the species had been cultivated in rich garden soil for several generations."

Misunderstanding V—*Mistaking re-infection for transmission.*—A particular form of the fourth misunderstanding has to do with facts so special that it may be conveniently treated of separately. It has to do with microbic diseases. It is ad-

mitted that a parent infected with tubercle-bacillus or with the microbe of syphilis may have offspring also infected. But such cases are irrelevant in the discussion. Infection, whether before or after birth, has nothing to do with inheritance. As Dr. Ogilvie says (1901, p. 1072), "Wherever the transmission of infectious disease from parent to offspring has been adduced to support the doctrine of the inheritance of acquired characters, it has been done in utter misconception of its meaning and scope."

Medical men have sometimes condescended to make a subtle distinction between "hereditary" and "congenital" syphilis—the latter manifested at birth, the former some time afterwards! It seems strange that they have failed to recognise that there is no reason to use the word "hereditary" at all in this connection. What occurs is an *infection*, and it is theoretically immaterial at what stage the infection occurs.* A microbe cannot be part of an inheritance.†

Misunderstanding VI—*Transmission in unicellulars is not to the point.*—It is not to the point to cite cases where unicellular organisms, such as bacteria or monads, have been profoundly and heritably modified by artificial culture, so that, for instance, the descendants of a virulent microbe have been made to lose their evil potency. It is irrelevant because in regard to unicellular organisms we cannot draw the distinction

* It may be the germ-cells that are infected—especially when the direct source of infection is the father; or it may be the embryo that is infected through the placenta: but the difference in the time of the infection is of no theoretical interest, nor can it be inferred from any difference in the outward symptoms, as these appear in the offspring.

† The egg of the green freshwater polyp (*Hydra viridis*) always contains little greenish corpuscles which are not present in the youngest stages of oogenesis. It is almost certain that these are minute unicellular Algæ (*Zoochlorellæ*). But no one can regard these useful symbions as actually part of the inheritance. The eggs of the silk-moth are often infected by a minute but fatal Protozoon which is present in the body of the moth. It seems uncertain at what precise point these pebrine organisms become associated with the egg, but however early it may be, the infection has nothing to do with inheritance. (See Ziegler, 1905, p. 5.)

between body and germinal matter, apart from which the concept of modifications is of no value. In artificial culture the whole character of the unicellular organism—its particular metabolism—is altered; it multiplies by dividing into two or more parts, which naturally retain the altered constitution. But this is worlds away from the supposed case of an alteration in the structure of the little toe so affecting the germ-cells that the offspring inherit a corresponding deformation.*

Prof. Adami (1901, p. 1319) says: "By subjecting a growth of pigment-producing bacteria to the action of a temperature just below that which will cause their death, we can bring about a loss of pigment production, so that the rapidly-succeeding generations are perfectly colourless; but gradually, in the course of time, the cultures made from the original (heated) tube regain the power of pigment production. This may be in two or three days, or, again, only after several transplantations at the end of two or three weeks; and when we remember that a bacillus divides and so forms a new generation in, on the average, something considerably less than an hour, it is seen that the acquired character may be impressed upon a race for some hundreds of generations. The more intense the alteration to which the bacillus is subjected, the longer and the more frequently the race is subjected to the altered temperature conditions, the longer it is before there is a sign of return to the normal."

These are interesting and reliable facts, but their citation as evidence of the inheritance of "acquired characters" is misleading, since no bacilli show any hint of the distinction between somatic and germinal material on which the definition of "acquired characters" depends, nor do they multiply except by division and

* It is surprising that even Prof. Oscar Hertwig (1898) supports his argument in favour of the transmissibility of somatic modifications by citing cases of inheritance in unicellular organisms. We are told that the irritability of certain Algae to light may be modified by exposure to strong light and to high temperature, and that "nobody would be surprised" if the progeny also showed "some similar property." But this is hardly evidence of the transmission of a modification! We are also told that under artificial conditions some bacteria may lose their toxic properties, and may transmit this somewhat negative character of lost virulence. This is admitted by all, but it is an *ignoratio elenchi*.

spore-formation. What occurred in the cases referred to was probably a temporary dislocation or disturbance of the characteristic organisation of the cells, with the result that pigment production was suppressed. When the inhibiting conditions were removed the original organisation recovered itself in the course of generations. But there is a great difference between such cases and, let us say, the transmission of sun-burning, or of specially strong muscles, or of a callosity on the skin, or a dwarfed form, which are instances of bodily modifications, technically called acquired characters. In the case of the bacilli the disturbed organisation was halved or multiplied in each reproductive process, and the effect originally induced was inherited from generation to generation, eventually disappearing as the restoration of normal conditions allowed the original organisation to re-assert itself in its integrity; in the case of the supposed inheritance of a callosity we have to assume either that the influence which induced this, or the influence of it after it had been induced, also affected the germinal material in the reproductive organs in such a way that the contained germ-cells, when liberated, developed into an organism with more or less of the callosity. It must be evident, without further discussion, that the cases are not at all on a par, and that inheritance in unicellulars has not been considered with sufficient carefulness even by experts.

Prof. L. Errera (1899) reported an experiment with a simple but multicellular mould (*Aspergillus niger*), which adapted itself to a medium more concentrated than the normal. The second generation of the mould was more adapted than the first, and the adaptation to the concentrated medium was not wholly lost after rearing in the normal medium again. This looks like evidence of the inheritance of the acquired adaptive quality which was brought about as a direct modification. But the case does not really help us, since the distinction between *soma* and *germ-plasm* is not more than incipient in the mould in question. And even if the distinction were more marked, it would only show that the germ-plasm is capable of being affected *along with* the body, by a deeply saturating influence, which nobody as ever denied.

Misunderstanding VII—*Changes in the germ-cells along with changes in the body are not relevant.*—Another misunderstanding is due to a failure to appreciate the distinction between a change of the reproductive cells along with the body, and a change in the reproductive cells conditioned by and representative of a particular change in bodily structure. The supporters of the hypothesis that modifications may be transmitted point to the tragic cases where some poisoning of the parent's system, by alcohol, opium, or some toxin, is followed by some deterioration in the offspring. There is no doubt as to the fact; the question is as to the correct interpretation.

(1) In some cases it may be that the whole system of the parent is poisoned—reproductive cells as well as body; the effect may be as direct on the germ-cells as on the nerve-cells. These, therefore, are not cases on which to test the transmissibility of an acquired character—*i.e.* of a particular somatic modification. If a local poisoning had a structural effect on some particular organ, and if that structural effect was reproduced in any degree in the offspring, the case would be relevant; but when the whole organism is soaked in a poison the case is irrelevant. If it could be said that the sunshine, which brings about sun-burning in the skin, soaks through the organism even to its reproductive cells and specifically affects them, in a manner analogous to the saturating poison, we should have a physiological basis for expecting the inheritance of sun-burning. But we cannot make this assumption. We have no warrant for believing that the modification of a part re-echoes in a definite specific way through the organism until even the penetralia of the germ-cells reverberate.

(2) A parent organism is poisoned, and there are structural results of that poisoning. The offspring are born poisoned, and show similar structural peculiarities. This may be due to the fact that the germ-cells were poisoned along with the parental body; but it may also be due, in the case of a mother,

to a poisoning of the embryo before birth, in a manner comparable to pre-natal infection.

(3) In some cases—*e.g.* of alcoholism in successive generations—there may be poisoning of the germ-cells along with the body, there may be poisoning of the embryo before birth, and of the infant after; but it may also be that what is really inherited is a specific degeneracy of nature, an innate deficiency of control, perhaps, which led the parent to alcoholism, and which may find the same or some other expression in the child.

Cases are known in which the children of a dipsomaniac father and a quite normal mother have exhibited a tendency to alcoholism, insanity, and the like. In this case the possibility of poisoning the unborn child is eliminated, but there remain three possibilities of interpretation,—that there was specific poisoning of the paternal germ-cells; that what was inherited was the constitutional weakness which expressed itself as alcoholism in the father; and that there were detrimental influences in the early nutrition, environment, education—"nurture," in short—of the offspring.

But while we have admitted a good deal, we have not admitted the transmissibility of a particular structural modification brought about in the parental body as a result of the toxin.

An illustration of what we mean by the distinction "along with, but not through the body," is afforded by an experiment of Paul Bert's. He tried to acclimatise some Daphniæ (small fresh-water crustaceans) to salt water by gradually adding salt to the aquarium. At the end of forty-five days, when the water contained 1·5% of salt, all the adults had died; but the eggs in their brood-chambers survived, and the new generation arising from these flourished well in the salt medium (*cit.* Packard, 1894, p. 345). Packard sees in this case an argument for the heritability of a modification, but it seems to us merely an instance of the direct modification of the germ-cells or of the embryos. Cuénot, whom Packard cites, gives the correct interpretation: "This experiment shows with admirable clearness that the germ-plasm has, owing to the modifi-

cation, become accustomed to the salt, causing it to produce a generation so different from the preceding."

Misunderstanding VIII—*Failure to distinguish between the possible inheritance of a particular modification and the possible inheritance of indirect results of that modification, or of changes correlated with it.*—At first sight this seems hair-splitting, but it is a crucial point. Through his vigorous exercise the blacksmith develops a muscular arm worthy of admiration; the shoemaker acquires skeletal and muscular peculiarities less admirable. There are many permanent and profound modifications associated with particular occupations. Are we to believe, it is asked, that the occupation of the parents has no influence on the offspring? Are we to believe, it is asked, that the children of soldier, sailor, tinker, tailor, are in no way affected by the parental functions?

It would be interesting to have precise data in regard to this, but it is generally admitted that when parents have healthful occupations their offspring are likely to be more vigorous. The matter is complicated by the difficulty of estimating how much is due to good nurture before and after birth. It is not unlikely, too, that some profound parental modifications may influence the general constitution, may even affect the germ-cells, and may thus have results in the offspring. But unless the offspring show peculiarities *in the same direction* as the original modifications, we have no data bearing precisely on the question at issue.

A belief in the inheritance of modifications was perhaps expressed in the old proverb, "The fathers have eaten sour grapes, and the children's teeth are set on edge"—a proverb which Ezekiel with such solemnity said was not any more to be used in Israel. Now if "setting on edge" was a structural modification, and if the children's teeth were "set on edge" as their fathers' had been before them, there would be a presumption in favour of the transmission of this acquired character, though it would be still necessary to inquire carefully whether

the children had not been in the vineyard too. But if, as Romanes said, the children were born with wry necks, we should have to deal with the inheritance of an indirect result of the parents' vagaries of appetite, and not with any direct representation in inheritance of the particular modification produced in the paternal dentition.

Misunderstanding IX—*Appealing to data from not more than two generations.*—It has often been pointed out that animals transported to a new country or environment may exhibit some modification apparently the result of the novel influence, and that their offspring in the same environment may exhibit the same modification *in a greater degree.* Thus sheep may show a change in the character and length of their fleece, and their progeny may show the same change more markedly.

But it is perfectly clear that if the evidence does not go beyond this, nothing is proved that affects the question at issue. It was to be expected that the offspring should show the modification in a more marked degree than their parents did, since the offspring were subjected to the modifying influences from birth, whereas their parents were influenced only from the date of their importation.

What would be welcome is evidence that the *third* generation is more markedly modified than the second; then there would be data worth considering. Only then would it be necessary to consider Weismann's somewhat subtle discussion as to the influence of climate.

§ 5. *Various Degrees in which Parental Modification might affect the Offspring*

It may seem, at first sight, unscientific to discuss various hypothetical degrees in which parental modifications might affect the offspring, when we do not know that modifications can be in *any* degree transmitted. But unless we are greatly mis-

taken, our theorem, if carefully attended to, will serve to make the issue clearer.

In regard to germinal variations, whose transmissibility is undoubted, it is well known that there may be different degrees of transmission, or, more cautiously stated, that the offspring's hereditarily determined reproduction of the parental variation may have diverse expressions. It seems just, therefore, to imagine that there might be different degrees in the transmission of modifications.

(1) The *first degree* of transmissibility would be illustrated if the offspring showed in any measure the same modification as the parent had acquired. If the sun-burnt parent had a congenitally swarthy child, that might be an indication of modification-transmission of the first degree of directness. It might be an illustration of what has been so carefully searched after—the transmission of *a particular acquired character.* We cannot too strongly emphasise that this and nothing else is what Weismann has denied; this and nothing else is the *crux* of "the interminable argument." And for the sake of argument, the possibility (1) must be kept quite distinct from the possibilities (2) and (3).

(2) If the offspring exhibited a new character, not the same as the parent's acquired modification, but affecting similar tissue, though in a different fashion, we might be justified in speaking of this as modification-transmission of the *second degree* of directness. It might be an illustration, not of the inheritance of a particular acquired character, but of something correlated therewith, if the much sunburnt parent of a thoroughly blond stock had a child with very dark hair on a very white skin. But the inference would not be certain.

(3) If the offspring exhibited a novel character, analogous to a modification, yet neither similar to the modification acquired by the parent nor affecting the same region of the body, it might be said that we had to deal with modification-inheritance of

the *third degree* of directness. It might be an illustration of the inheritance of an indirect effect of a parental modification if the sons of fathers who had eaten sour grapes had wry necks. But we should require many instances before admitting the hereditary nexus.

§ 6. *The Widespread Opinion in favour of Affirmative Answer*

It seems to be a widespread opinion that acquired characters may be transmitted, but often the opinion wavers when it is explained what this precisely means—namely, that a modification in the body, brought about by a change in function or environment, may so specifically affect the reproductive elements that when these develop there is in the offspring something corresponding to the parental modification.

Opinion of " Practical Men."—In fairness we must admit that the verdict of the *practical* man, whether physician or breeder, gardener or farmer, is still in many cases an unhesitatingly affirmative answer. One of the keenest of physicians has said that a few months in practice would dispel all doubt as to the inheritance of acquired characters ; but there are equally keen physicians who have taken a different view. It may also be that the first had not freed himself from Misunderstandings V and VII.

Prof. Brewer, an American authority on breeding, who gives an emphatic affirmative answer, notes:

" The art of breeding has become in a measure an applied science ; the enormous economic interests involved stimulate observation and study, and what is the practical result ? This ten years of active promulgation of the new theory has not resulted in the conversion of a single known breeder to the extent of inducing him to conform his methods and practice to the theory. My conclusion is that they are essentially right in their deductions founded on their experience and observations—namely, that ac-

quired characters may be, and sometimes are, transmitted, and that the speculations of the Weismann school of naturalists are unfounded."

But perhaps this widespread opinion does not mean so much as it seems; for it is very difficult to get busy practical men to take the trouble to appreciate an exact distinction such as is involved in the phrase, "the inheritance of an acquired character."

Against the opinion quoted we may balance that of an experienced botanical physiologist, Prof. MacDougal. "Despite general assertions to the contrary, no evidence has yet been obtained to prove that the influence of tillage, 'cultivation,' or the mere pressure of environment factors has produced any permanent changes in hereditary characters of unified strains of plants."

Great Variety of Opinion.—There is little to be gained by a citation of opinions, for there are equally authoritative names on both sides. But there are some points of interest. Thus we have already noticed that the scepticism as to the inheritance of acquired characters is not a modern fad. It is also noteworthy that, while the majority of zoologists disbelieve in modification-inheritance, the reverse seems to be the case with botanists. Is this because modifications are even more marked and more recurrent in plants than in animals, or because the distinction between soma and germ-plasm is much less definite in plants than in animals?

But there is this use at least in noting the discrepancy of opinions, that we are warned from dogmatism. It cannot be an easy question when we find Spencer on one side and Weismann on the other, Haeckel on one side and Ray Lankester on the other, Turner on one side and His on the other, and so on.

Herbert Spencer was so convinced that he went the length of writing: "Close contemplation of the facts impresses me more strongly than ever with the two alternatives—*either there*

has been inheritance of acquired characters, or there has been no evolution." *

Haeckel is so convinced for the affirmative that he stakes his particular form of religion upon it, asserting that "belief in the inheritance of acquired characters is a necessary axiom of the monistic creed"; and what may sound to some even more serious is his declaration that, rather than agree with Weismann in denying the inheritance of acquired characters, "it would be better to accept a mysterious creation of all the species as described in the Mosaic account."

Sir William Turner has said that "to reject the influence which the use and disuse of parts may exercise, both on the individual and on his offspring, is like looking at an object with only a single eye"—which is not perhaps a very emphatic condemnation, since most microscopic research is monocular. Moreover, the doyen of British anatomists does not state the case with his usual precision.

Why is the Affirmative Position so widely held?—Even in regard to our own muscular and nervous systems, we are familiar with illustrations of the fact that practice increases capacity, and that desuetude is apt to be followed by loss of power. *A force de forger on devient forgeron.* Organs improve with the using and deteriorate in disuse. We are also well aware that changes in the environment or conditions of life, and notably in our food, cause changes in our body. It seems a "natural" assumption to suppose that these gains and losses and changes may be in some degree transmissible.

Apart from the "naturalness" of this assumption, there are probably four reasons why the affirmative position is so widely held:

(1) There are many facts which *suggest* modification-inheritance

* The italics are ours. See Herbert Spencer, "The Inadequacy of Natural Selection," *Contemporary Review*, February and March, 1893. Appendix B, *Principles of Biology*, 2nd ed. vol. i. 1898, p. 621.

until they are examined critically. The late Duke of Argyll, in one of his scientific excursuses, said the world was strewn with illustrations of the inheritance of acquired characters, and Dr. W. Haacke, a very wide-awake evolutionist, has compared the evidences for the affirmative to the sand on the sea-shore for multitude, yet neither furnishes us, so far as we are aware, with a single case that will bear analysis. The affirmative may be an obvious interpretation of the results of evolution, but the obvious interpretation is seldom the right one. The sun does not go round the earth.

(2) The affirmative is an interpretation which seems to make the theory of organic evolution simpler ; it suggests a more direct and rapid method than the natural selection of germinal variations. If to a growing and varying nature or germinal inheritance there were continually being added the results of peculiarities in nurture, the rate of evolution would be quickened, both upwards and downwards. But our first business is to find out whether the hypothesis actually consists with experience.

Dr. Walter Kidd has argued carefully and ingeniously that all departures of hair-direction from a simple and primitive type *may be interpreted* as due to mechanical causes, namely, stimuli repeated immensely often. The difficulty here and always is with the presuppositions of the interpretation.

(3) We are so accustomed in human affairs to the entailment of acquired gains from generation to generation, to standing on the shoulders of our ancestors' achievements, that many find it difficult to refrain from projecting this on organic nature. They forget that the greater part of our entailing process comes about through our *social heritage*, which is altogether apart from our *natural inheritance*.

(4) A fourth reason is that many fictitious or anecdotal cases of the inheritance of acquired characters continue circulating. The inheritance of a letter branded upon the arm, which Aristotle notes, is still in the popular currency, though it is perhaps an

extreme type of what His calls a handful of anecdotes. It is reported that Sioux Indians tattoo discs on the cheekbone prominences of their squaws, and it is said that similar marks may be seen on some new-born children (*Nature*, iii., 1870, p. 168). And besides fictitious cases there *are* some puzzling phenomena, which the supporters of the negative position are wont to dismiss as "coincidences"—which, it must be confessed, is never a very satisfactory way of dealing with difficult cases.

§ 7. *General Argument against the Transmissibility of Modifications*

Most of the evidence brought forward in support of the belief in the inheritance of acquired characters is terribly anecdotal; but apart from this Weismann was led to a position of entire scepticism by his realisation of the continuity of the germ-plasm.

The Apartness of the Germ-cells.—If the germ-plasm or the material basis of inheritance be something relatively apart from the body, and from its everyday metabolism, something often segregated at a very early state in development, there is a presumption against its being readily affected in a specific manner by detailed exogenous changes wrought on the structure of the body.

It seems accurate to say that the reproductive cells which have the potentiality of becoming offspring never arise from differentiated body-cells. Whether they are recognisable as such, late or early, the germ-cells are simply those cells which retain in all its integrity the complex, definite, and stable organisation of the fertilised ovum from which the whole organism develops. They have their power of reproducing creatures more or less like the parents just because they are continuous, through an unspecialised cell-lineage, with the fertilised ovum from which the parental body arose. All the somatic cells are, of course, likewise the progeny of the fertilised ovum; but in their lineage there is differentiation and specialisation. We imagine that in them the numerous items or potentialities in the fertilised

ovum are distributed and allowed to express themselves. In the germ-cell lineage they are kept concentrated and latent.*

In any case the germ-cells in the reproductive organs are not actively functioning elements of the body; they are in a quite peculiar way apart from the general soma; and Weismann has reasonably emphasised the difficulty of picturing any means whereby the modification of a particular corner of the body can react upon the germ-cells in a manner so specific that these can, when they develop, reproduce the particular parental modification or any approach to it. This argument, and the answers to it, must be carefully considered.

1. **The Germ-cells may be affected by the Body.**—In the first place, it has been answered that the body does undoubtedly, in some cases, exert some influence on the gonads, so that the difficulty is reduced to this: Can a modification of part of the body exert a specific or representative influence on the germinal material?

But what is the precise nature of the alleged influence of the body on the gonads? It is pointed out that nervous changes can excite the reproductive organs, that food-stuffs may increase their activity, that alcohol and other stimulants may influence them, and so on. But there is a great difference between any such excitation of the gonads and the propagation of a particular modification, let us say, from the skin to the germ-cells. And there is a great difference between a poisoning of the germ-cells along with the body, and the influencing of them in a manner so specific that they can, when they develop, reproduce the particular parental modification. (*See* Misunderstanding VII.)

* In certain conditions, as yet unknown, certain body-cells may revert to a primitive mode of behaviour—like some kinds of criminals in society. Thus the cells which develop into cancerous growths behave in some ways like germ-cells, especially in their mode of division. (See the researches of Farmer, Walker, and Moore.) But such cases need not lead us to Hertwig's extreme conclusion that every cell is potentially a germ-cell.

2. **Hypotheses as to Possible Mechanism of Transmission.**— In the second place, attempts have been made to construct hypotheses by aid of which we might conceive how a modification of, say, the skin, can exert a specific or representative influence on the germinal material.

Thus, Darwin suggested his provisional hypothesis of pangenesis, according to which the parts of the body give off gemmules which pass as samples to the germ-cells. But his suggestion remains a pure hypothesis—and an unnecessary one unless new facts come to light—and is nowadays maintained by no one except in extremely modified form—*e.g.* in the Pangen-theory of De Vries.

Spencer deserves credit for at least facing the difficulty of conceiving a *modus operandi* whereby a particular modification in, say, the brain or the thumb, can specifically affect the germinal material in such a way that the modification or a tendency towards it becomes involved in the inheritance. Briefly stated, his theory is as follows:

Spencer's Theory of the Mechanism of Transmission.—Spencer made the legitimate postulate that, intermediate between the biological unit or cell and the chemical molecule, there were "constitutional units," the vehicles of specific characters, ancestral and parental traits, and the individual peculiarities of the organism itself.

He supposed that they were very stable in their "fundamental traits," but plastic as regards their "superficial traits."

He supposed that they had "such natures that while a minute modification, representing some small change of local structure, is inoperative on the proclivities of the units throughout the rest of the system, it becomes operative in the units which fall into the locality where that change occurs."

He supposed "an unceasing circulation of protoplasm throughout an organism," such that, "in the course of days, weeks, months, years, each portion of protoplasm visits every part of the body"—a wild assumption.

Finally, "we must conceive that the complex forces of which

each constitutional unit is the centre, and by which it acts on other units while it is acted on by them, tend continually to re-mould each unit into congruity with the structures around, superposing on it modifications answering to the modifications which have arisen in these structures. Whence is to be drawn the corollary that in the course of time all the circulating units—physiological, or constitutional, if we prefer so to call them—visit all parts of the organism; are severally bearers of traits expressing local modifications; and that those units which are eventually gathered into sperm-cells and germ-cells (*i.e.* egg-cells), also bear these superposed traits."

Thus the constitutional units are supposed to circulate and to visit one another throughout the body. When they come to a modified structure and visit its modified constitutional units, they are supposed to be themselves impressed; thus impressed, they are supposed to be gathered into the germ-cells, which thus come to bear the "superposed traits" resulting from modifications.

If we were sure that modifications were ever transmissible, we might be glad of this hypothetic interpretation of the business. But it is a difficult hypothesis to think out, and it would hardly be tolerable even if there were facts which it was needed to interpret. In particular, the conception of "an unceasing circulation of protoplasm," so that "each portion of protoplasm visits every part of the body," seems not only unwarranted, but contradicted by well-established facts.

3. **A Mechanism may exist though it remains Unknown.**— In the third place, we must recall Prof. Lloyd Morgan's warning that although we cannot imagine how a modification might, as such, saturate from body to germ-cells, this does not exclude the possibility that it may actually do so. Oscar Hertwig also maintains that our ignorance of any mechanism which could secure the transmission of an acquired character is not a good argument against the possibility of its occurrence. There are, he says, many facts in biology which are quite secure, though no causal nexus can be worked out at present (*Allgemeine Biologie*, 1906, p. 621). It must be noted, however,

that, so far as we can understand, ***a very complex and special mechanism*** would be necessary if a modification in, say, the eye is specifically to affect the germinal material.

Dr. George Ogilvie (1901) writes: "In a subject so involved in obscurity the present incomprehensibility of certain relations can hardly serve as an argument against their existence. The development of the apparently uniform germ-plasm into the infinite differentiation of a complex cell-state is, although no longer a matter of doubt, perhaps not less inconceivable." But this illustration is not altogether appropriate, since our inability to conceive the precise "how" of development rests on our inability to restate in simpler terms any of the fundamental facts of life, such as growth, assimilation, or reproduction, whereas the supposed relation between soma and germ-cells is inconceivable in rather a different sense.

From various quarters—*e.g.* from Mr. J. T. Cunningham, Prof. Dendy, Prof. MacBride, Prof. Bergson—has come the interesting suggestion that structural changes in the body, brought about by peculiarities in nurture, may set free specific "hormones," which are diffused through the system and find representation in the germ-cells, in whose development they may eventually assert themselves.

A Concrete Case: Spencer's Hands.—It may illumine the abstract argument to take a concrete case. Why had Herbert Spencer small hands? He says that it was because his grandfather and father were schoolmasters, who did little manual work from day to day, save in wielding the pen and sharpening the pencil. Through disuse of the sword and the spade their hands were "directly equilibrated" towards smallness. But since Mr. Spencer senior was "a combination of rhythmically acting parts in moving equilibrium," the dwindling of the hands and the moulding of the physiological units thereof reverberated through the whole aggregate; a change towards a new state of equilibrium "was propagated throughout the parental system—

a change tending to bring the actions of all organs, reproductive included, into harmony with these new actions," or inactions. The modified aggregate impressed some corresponding modification on the structures and polarities of the germ-units. And this was how Herbert Spencer had small hands. At least, so he tells us.

Disuse of Parts.—It seems "natural" to suppose that organs have dwindled *pari passu* with their disuse, and *because* of their disuse. But the two statements are not synonymous. The dwindling may be due to germinal variations in the line of reduction, which are appropriate because of some change in the animal's habits and environment. It may even be that the organism meets an endogenous reduction of certain parts by itself changing its habits and habitat. Moreover, it is important to notice, as Emery, Kennel, and Ziegler have pointed out, that there has probably been a "Kampf der Theile im Organismus" (a struggle of parts within the organism) not merely in individual ontogeny, but also in the racial phylogeny. Dwindling of one part occurs when some adjacent part attains increased differentiation. "Thus snakes have not lost their limbs because they did not use them, but because of their evolution in the direction of exceptionally large trunk and tail musculature. In man the strong dentition of his Simian forebears has become weaker, not through disuse, but because the extraordinary increase of the brain has been correlated with a weaker development of other parts of the head" (H. E. Ziegler, 1905, p. 3).

§ 8. *General Argument for the Transmissibility of Modifications*

The Germ-cells are not Insulated.—While it must be admitted that the germ-cells have a certain apartness from the daily life of the body, and that they are unspecialised cells that have not shared in the differentiation characteristic of the body-cells, is there not some risk of exaggerating the distinction between somato-plasm and germ-plasm?

In many simple animals, such as sponges and hydroids, the germ-cells simply make their appearance at certain times of year among the commonplace somatic cells. In many plants the distinction between body and germ-cells can hardly be drawn until the period of reproduction sets in. Thus Spencer refused to accept the contrast between *body*-cells and *germ*-cells as expressing a fact, and referred to the numerous cases in which small pieces of a plant or a polyp may grow into entire organisms.

To this objection Weismann answers,—(1) that the distinction between somatic cells and germ-cells has been gradually emphasised in the course of evolution, and that in the simpler multicellular organisms it is still incipient; (2) that it is quite conceivable that, even in some complex organisms, the body-cells, though differentiated, may retain some residual unused germ-plasm; and (3) that there may be a quite definite and distinct germ-*plasm*, though there is no demonstrably distinct lineage of germ-*cells*.

Again, however, we must remember that the blood, or lymph, or other body-fluids form a common medium for all the parts of the animal, gonads included; the results of changes in nutrition may saturate throughout the body and affect the germ-cells *inter alia*. The nervous system makes the whole organism one in a very real sense; in plants there are often intercellular bridges of protoplasm binding cell to cell, and this is true in not a few cases among animals. Moreover, there are subtle, dimly understood correlations between the reproductive organs and the rest of the system. If changes in the reproductive organs can effect changes in remote parts, such as the larynx and the mammary glands, why may not there be reciprocal influences? In short, the organism is a unity, and to divide it up, in any hard-and-fast way, into soma and germ-cells may land us in the same fallacy as parcelling the mind into separate faculties.

It must be admitted, therefore, that it is quite erroneous to think of the germ-cells as if they led a charmed life, uninfluenced

by any of the accidents and incidents in the daily life of the body which is their bearer. But no one believes this, Weismann least of all, for he finds the chief source of germinal variations in the stimuli exerted on the germ-plasm by the oscillating nutritive changes in the body.

Weismann's Concessions.—There are some who find in this "a concealed abandonment of the central position of Weismann," and who say: "If the germ-plasm is affected by changes in nutrition in the body, and if acquired characters effect changes in nutrition, then acquired characters or their consequences will be inherited." But it is quite illegitimate (§ 5) to slump acquired characters and their consequences as if the distinction were immaterial. The illustrious author of *The Germ-Plasm* has made it quite clear that there is a very great difference between admitting that the germ-plasm has no charmed life, insulated from bodily influences, and admitting the transmissibility of *a particular acquired character*, even in the faintest degree. The point, let us repeat, is this: Does a structural change in a part of the body, induced by use or disuse, or by change in surroundings, influence the germ-plasm in such a specific or representative way that the offspring will thereby exhibit the same modification that the parent acquired, or even a tendency towards it?

The Real Difficulty.—Even when we recognise, as fully as we can, the unity of the organism, that each part shares in the life of the whole, it is very difficult to think of any *modus operandi* whereby a local modification can specifically affect the germ-plasm. The argument that we can as little understand the *modus operandi* whereby an influence passes from the gonads to distant parts of the body is not really sound. For we know that in some cases the reproductive organs, besides being areas for the multiplication of germ-cells, are organs of internal secretion, producing specific substances which are carried away by the blood-stream, and serve as the stimuli awakening the dormant potentialities of distant parts.

Nor does the fact that morbid processes in a particular part may result in a diffusion of toxins, which saturate even the germ-cells, help us much in our attempt to picture how a modification could become transmissible. For there is not the slightest reason for supposing that the ordinary modifications in which naturalists are interested, which experimental evolutionists can bring about, are associated with the formation of specific toxins which might diffuse through the whole system.

Spencer's Statement of the a priori *Argument.*—As Herbert Spencer was perhaps the keenest and most convinced upholder of the affirmative position, it seems just to give his statement of the *a priori* argument. We have made a comment on each of the steps.

(1) "That changes of structure caused by changes of action must be transmitted, however obscurely, appears to be a deduction from first principles—or if not a specific deduction, still, a general implication."

"For if an organism, A, has, by any peculiar habit or condition of life, been modified into the Form A^1, it follows that all the functions of A^1, reproductive function included, must be in some degree different from the functions of A."

"An organism being a combination of rhythmically acting parts in moving equilibrium, the action and structure of any one part cannot be altered without causing alterations of action and structure in all the rest."

Comment.—(*a*) It is not denied that some deeply saturating modifications of the body, affecting the nutritive stream, may affect the reproductive organs. This is not the point at issue. (*b*) How far a modification is likely to affect the reproductive organs must be determined by observation and experiment. The appreciability of the change will depend on the amount and nature of the modification, and on the intimacy of the correlation subsisting in the organism. Dislodging a rock may alter the centre of gravity of the earth, but it does not do so appreciably.

(2) "And if the organism A, when changed to A^1, must be changed in all its functions, then the offspring of A^1 cannot be the same as they would have been had it retained the form A."

Comment.—This is logical, but is it true? The change from A to A^1 may be important, it may appreciably alter the

metabolism, but it does not follow that it can appreciably alter the architecture of the germ-plasm. Spencer's assumption that the change in the constitutional units of the body must affect the constitutional units in the germ-cells remains an assumption.

(3) "That the change in the offspring must, other things equal, be in the same direction as the change in the parent, appears implied by the fact that the change propagated throughout the parental system is a change towards a new state of equilibrium—a change tending to bring the actions of all organs, reproductive included, into harmony with these new actions."

Comment.—It seems to us to pass the wit of man to conceive how or why an improved equilibrium in, let us say, the use of the hand should involve any corresponding or representative change of equilibrium in the germinal material. The drawback to abstract biology based on first principles is that it enables its devotees to develop arguments which seem plausible until they are reduced to the concrete.

§ 9. *Particular Evidences in support of the Affirmative Answer*

The question is whether modification-inheritance does or does not occur, and we must no longer postpone our consideration of the concrete evidence used to support the affirmative position. Our reason for not placing this section in the foreground of the chapter is mainly that a multitude of misunderstandings have had to be cleared away before the so-called direct evidence could be profitably considered. When one naturalist, Dr. W. Haacke, declares that instances of modification-inheritance are as plentiful as sand on the shore, and another, Prof. E. Ray Lankester, declares that the Lamarckian position has its only remaining defence, and that no secure one, in Brown-Séquard's experiments, we have obvious justification for our preliminary discussion.

The instances adduced as evidence of modification-inheritance might be classified according to the errors involved, but we have arranged them rather in reference to the general nature of the modifications discussed, whether environmental or functional,

whether tending to increase or decrease, and so on. The alleged inheritance of the direct effects of mutilations, injuries, and the like is discussed separately in §§ 10 and 11.

Improvement in Trotting Horses.—Over a hundred years ago (1796) the utmost speed of the English trotter was stated at a mile in 2 min. 37 sec. Since 1818, accurate records have been kept, which show a gradual increase decade after decade in the speed and in the percentage of swift trotters. The standard has risen and the breed has improved. The mile can now be run in 1 min. 54 sec. There has been an improvement of nearly 30 per cent. in 70 years. It is claimed that we have here direct evidence of the transmission of the structural results of exercise.

Brewer (*cit.* Cope, 1896, pp. 426-30) relates that about 1818 the record speed of the trotting horse was 3 min. to the mile; in 1824 it was reduced to 2 min. 34 sec.; in 1848, to 2 min. 30 sec.; in 1868, to 2 min. 20 sec.; in 1878, to 2 min. 16 sec.; in 1888, to 2 min. 11½ sec.; and finally to 2 min. 10 sec. "The gain in speed has been cumulative. . . . It has gone on along with systematic exercise of special function in successive generations; . . . there is nothing that would lead us to even suspect that the changes due to exercise of function had *not* been a factor in the evolution; . . . there is every appearance and indication that the changes acquired by individuals through the exercise of function have been to some degree transmitted, and have been cumulative, and that this has been one factor in the evolution of speed."

The increase of speed has been partly due to improvements in the light vehicle or "sulky," in the track, in the individual training, but partly to improvement in the blood. The interpretation of the result simply by the hypothesis of use-inheritance gives a false simplicity to the case. It overlooks the rigorous selective breeding which increases the constitutional swiftness,

and the process of elimination which persistently weeds out the less swift from the stud. And even apart from artificial selection and elimination there may be a progressively cumulative succession of *variations* making for greater and greater swiftness. We may even picture how this might come about, if we adopt Weismann's conception of germinal selection.

Case of Squatting Punjabis.—It has been stated that the Punjabis of India show certain peculiarities of musculature and skeleton which are associated with the frequency with which these people assume on all possible occasions the squatting posture. It is asserted that the peculiarities of structure are due to the peculiarities of function, but this requires definite proof (Misunderstanding III). They may be adaptations originating in germinal variations. It is stated by Charles (*Journ. Anat. and Physol.*, vol. 25) that the peculiarities in question are indicated even in the fœtus. This is interesting and important, but there can be no conclusiveness in regard to peculiarities whose first appearance is hidden in obscurity. If squatting increased from generation to generation, and if the structural peculiarities increased *pari passu*, the case would be interesting; but even then we should have to inquire whether we were not dealing with a progressive variation.

Peculiarities of Occupations.—In his interesting paper on the anatomy of the shoemaker, Dr. Arbuthnot Lane describes the peculiarities induced by this occupation, which tends to form a distinct anatomical type. The same is true of the tailor. "The bent form, the crossed legs, thumb-and-forefinger action, and peculiar jerk of the head while drawing the thread, are the main features of the sartorial habit," and they are associated with permanent changes in muscles, insertion surfaces, and articulations. These are indubitable modifications: what of their transmission? No one, Dr. Lane says, would expect any perceptible changes in the first generation, but he thinks that he has observed inherited effects in the third.

We can only say that this line of inquiry deserves to be followed up, especially since our minute acquaintance with the human body and the accumulation of facts in regard to its variations make a discrimination between modification and variation more secure than is possible in many other cases. It should be remembered, however, that if the shoemaker's sons and grandsons and subsequent descendants all "stuck to the last," there might tend to be an accumulation of general constitutional peculiarities —*e.g.* of meditativeness and of the physical effects of persistent sedentary work, which might dispose the organism to re-acquire particular modifications in a more marked degree.

Large and Small Hands.—Darwin (*Descent of Man*, p. 18) refers to the alleged fact that the infants of labourers have larger hands than those of the children of the gentry; but this, and many similar cases of which it is a type, may be sufficiently accounted for by interpreting the observed differences as constitutional characteristics of different stocks probably accentuated by various forms of selection. Spencer notes, "That large hands are inherited by those whose ancestors led laborious lives, and that those descended from ancestors unused to manual labour commonly have small hands, are established opinions." But if we accept the "opinions" as correct, it is easy to interpret the size of the hands as a stock character correlated with different degrees of muscularity and vigour, and established by selection. The hands of Japanese are in many details anatomically different from the hands of Europeans, but there is no warrant for regarding these detailed differences as other than constitutional racial differences of germinal origin accentuated modificationally in the individual lifetime.

Dwindling of Little Toe.—The alleged dwindling of the little toe has been repeatedly cited as a case in point—proving the inheritance of a modification produced by tight boots. But precise data are wanting; a dwindling has also been observed in savages who do not wear boots; it is possible that there may

be in man, as there was in the ancestors of the modern horse, a constitutional variation in the direction of reducing digits; and there are other possible explanations of the rather vague assertions. It need hardly be pointed out that unless there is a measurably *progressive* dwindling with similar boots in the course of generations the case has no point. A control experiment comparing the toes in sets of brothers respectively booted and bootless would be interesting.

Results of Pressure.—Darwin (*Descent of Man*, p. 18) regards the thickened sole of even unborn infants as due to "the inherited effects of pressure during a long series of generations." But here again it is impossible to exclude the interpretation that a variation in the direction of thickened solar epidermis might have selection-value from very ancient days, to the arboreal ape as well as to the bootless man. H. H. Wilder, in a paper in which he gives a detailed comparison of the palms and soles of Primates and Man (*Anat. Anzeig.* xiii. (1897), pp. 250-6), distinctly refuses to commit himself to a Lamarckian theory, believing that the facts may be equally well interpreted in terms of variation and selection.

Bollinger (1882) suggests that the weak development of the breasts in women of the Dachauer district is due to the old-established fashion of wearing tight corsets which are pressed flat on the breasts. It is necessary to inquire (*a*) whether the peculiarity is not a modification inflicted on each successive generation, or whether it is ever exhibited by a Dachauer woman who does not wear a corset; and (*b*) whether the same peculiarity does not occur where the fashion is entirely different.

Climatic Changes.—Virchow and others have laid stress on the fact that many peculiarities in races of men and of other living creatures are climatic in origin, and yet are now part of the natural inheritance. But acclimatisation is usually a slow and gradual process, involving selection of germinal variations, and it is difficult to get clear-cut cases of climatic modifications.

It must also be remembered that Weismann expressly admits that climatic influences, especially if long-continued, may influence the germ-plasm along with the whole system, and may induce germinal variations that come to stay; but this "has certainly nothing to do with the view that functional modifications of any particular organ can cause a corresponding change in the germ-plasm." (See *The Germ-Plasm*, 1893, p. 408.)

In adjacent areas with different climatic and other environmental conditions we not infrequently find closely related species or local races. It seems impossible to doubt that these are blood-relations, derived from a common ancestor. Are they not due to the environmental differences? In some way, surely, the organismal differences are causally correlated with the environmental differences, and it is granted by all that peculiarities of climate induce changes in the nutrition, respiration, circulation, and so on. If so, the germ-plasm may be affected and variations may be provoked, some of which are adaptive. But the result of these variations may be something different from and much more profitable than the modifications directly induced. They may be expressed in relation to quite different organs. Thus it seems quite unnecessary to believe in the transmission of climatic modifications as such, or in any representative degree. Moreover, we must never forget that the active organism must be credited with the power of seeking out environments which suit its inborn nature—variations included.

Plants in New Environment.—Much has been made of the changes which follow a radical change of environment. When a plant is transferred to a new soil and climate it may undergo a very marked change of habit; its leaves may become hairy, its stem woody, its branches drooping. "These," Herbert Spencer said, "are modifications of structure consequent on modifications of function that have been produced by modifications in the actions of external forces. *And as these modifications reappear in succeeding generations, we have, in them, examples*

of functionally established variations that are hereditarily transmitted. But this is a *non-sequitur*, since the modifications may reappear merely *because they are re-impressed directly* on each successive generation. It is Misunderstanding IV.

At the same time it should be noted that radical change of environment may induce germinal variations or mutations which breed true. These must be distinguished from modifications, as already explained, since we cannot interpret them physiologically as the direct somatic results of the environmental change.

Another case requiring consideration is that of a Turkestan relative of our common Shepherd's Purse (*Capsella bursa pastoris*). It has apparently spread from the low country to the uplands, and the specimens growing at the higher altitudes are smaller than those below, and pink instead of white. Seeds of lowland forms sown in the uplands develop into small plants with pink flowers, but the upland forms keep their characters (except the xerophytic leaves) when grown in the low country. It is possible that we have here to do with a variation coincident with a modification; it seems, however, that the experiments require to be repeated and extended.

Experiments on Brine-shrimps.—Reference is often made to the observations and experiments of Schmankewitsch (1875) on certain brine-shrimps belonging to the genus *Artemia*. By lessening the salinity of the water he was able to transform one type, *Artemia salina*, in the course of generations into another type, *Artemia milhausenii*. By increasing the salinity, he was able to reverse the process. Although he did not himself make any such claim, his work has often been referred to as an illustration of changing one species into another, and of the inheritance of acquired characters.

It seems very doubtful, however, whether we have here to do with modifications at all. Schmankewitsch did not modify any one *Artemia salina* into *Artemia milhausenii*; with a progressively changing environment and in the course of generations he observed a transition of the population from the one type to the other; it is probable that the change of salinity operated

directly on the eggs. This seems the more likely since the differences between the two types (in shape of tail, details of bristles, etc.) are not such as we can interpret as the natural direct results of altered salinity. It is well known that slight alterations in the physico-chemical composition of the water have sometimes a great and mysterious influence on eggs and developing embryos.

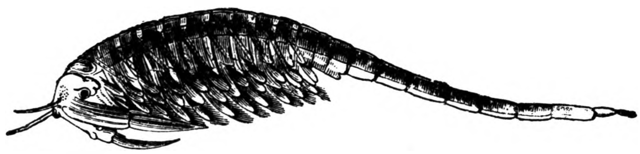

FIG. 27.—Side view of male *Artemia salina* (enlarged). (From Chambers's *Encyclopædia.*)

Bateson and others have shown that there is great variability in the character of the tail and bristles of *Artemia salina,* of which *A. milhausenii* seems to be only an extreme form without tail-lobes.

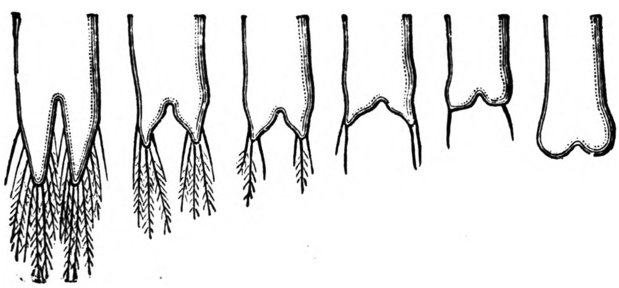

FIG. 27*a*.—Tail-lobes of *Artemia salina* (to the left) and of *Artemia milhausenii* (to the right); between these four stages in the transformation of the one into the other. (From Chambers's *Encyclopædia*; after Schmankewitsch.)

But if the changes were somatic modifications, it is still open to the critic to point out that Schmankewitsch experimented with a progressively changing environment on a series of generations, and that the results were due to modifications hammered afresh on each successive generation, without there being any inheritance of these modifications.

A Typical Case.—An often-quoted and typical instance was communicated to Darwin by Moritz Wagner. Some pupæ of a Texan species of *Saturnia* were brought in 1870 to Switzerland. In May, 1871, the moths emerged and were entirely true to type; they had young, and these were fed on the leaves of *Juglans regia* (the Texan form feeding on *Juglans nigra*); these young developed into moths so different in colour and form from their parents that some entomologists referred them to distinct species. This was a well-marked individual modification, but the story stops just where it was beginning to be interesting. We are not told about the subsequent generations. If they, too, were fed on *Juglans regia,* and reared in Switzerland, they probably reproduced the new type, but this would simply mean that the modification was re-impressed on successive generations.

Experiments on Lepidoptera.—Standfuss reared pupæ of *Vanessa urticæ* at a lower than the normal temperature, and obtained a northern type (var. *polaris*); he reared them at a temperature higher than the normal, and obtained a southern variety (var. *ichnusa*). In the progeny he found a very small percentage (all males) which showed a change in the same direction as the parents.

Fischer worked with *Arctia caja,* reared the pupæ at 8° C., and obtained some unusually dark forms. Two of these were paired and their progeny was reared at the normal temperature. A small percentage of these—the last of the brood to emerge from the pupa-state—showed the same kind of melanistic peculiarity as the parents had shown.

Fischer pointed out, however, that the colour-aberration in the offspring was not a repetition of the parental peculiarity, though it was in the same direction and sometimes went farther. He did not regard the case as illustrating the transmission of a specific modification, but agreed with Weismann's interpretation that the germ-cells had been prompted to vary by the lowered

temperature. It should also be noted that in many butterflies there is a strong constitutional—*i.e.* germinal—tendency to melanistic variation, that the aberration does not occur in all the individuals subjected to the low temperature, that it occurs in very diverse degrees, and that the experimenter *selected* two forms to pair together.

Fresh Experiments.—Among the twentieth-century experiments on the transmission of modifications, there are a few which suggest that a dogmatic denial of the possibility is very unwise.

Kammerer has made some striking experiments on Amphibians (*Archiv. für Entwicklungsmechanik*, 1898–1914).

(1) He kept the spotted salamander (*Salamandra maculosa*) in the cold and got it, after a few births, to produce, instead of the usual numerous larvæ or numerous eggs, two young ones, *as in the black salamander* (*S. atra*) *of the Alps*. The offspring of these spotted salamanders kept in normal environment gave birth to very advanced larvæ—showing a partial persistence of a modified form of reproduction in the absence of the modifying conditions. Other results of the same kind were obtained.

(2) Young salamanders on a yellow floor became yellower than usual, and their offspring exposed to the same influences were yellower still. But some of these offspring *reared on a black floor* showed themselves yellower than usual for the first six months of their life, till the black pigment began to predominate.

(3) The Nurse Frog, Alytes, normally pairs on land, and the male has no horny pad on its hand for gripping the female. Kammerer induced the frog to pair in water, and after several generations males with swollen pads were produced.

(4) W. E. Agar (*Philosophical Transactions*, Roy. Soc., 1913) subjected a small water-flea (Simocephalus) to peculiar environment and induced a peculiar modification. After eggs had appeared and grown in the ovary, the little crustaceans were restored to normal water. In due time the eggs developed, but the offspring showed the parental modification. When the parents laid again, the abnormal feature was seen in the offspring in a slight degree ; in a third brood it had dwindled away. It is probable that the original peculiarity of nurture resulted in the production of some peculiar non-living metabolic product, which was included in the cytoplasm

of the egg, passed passively into the body that developed from the egg, and there produced on the body of the offspring the same effect as it originally produced on the body of the parent which acquired the peculiarity in question.

Breeders' Evidence.—The evidence given by breeders in support of the theory of modification-inheritance, which is a tacit or an avowed belief of many, if not of most, appears to us in most cases too full of vagueness and misunderstanding to be of significance; but it has been often adduced by expert biologists, notably by Cope (1896), who cites his cases from Brewer (1892–3), an acknowledged agricultural authority. The first argument relates to the inheritance of characters due to nutrition, and is as follows: The size of domestic animals is often of much practical importance, and has been attended to for many years with all the carefulness which a pecuniary stake ensures. It used to be said that "feed is more than breed," but it is now recognised that "heredity or 'breed' is the more important." There is also, of course, careful selection, "but no breeder claims that a breed is or can be kept up to extra size by selection alone." "Breeders do not believe that the characters acquired through the feeding of a single ancestor, or generation of ancestors, can oppose more than a slight resistance to that force of heredity which has been accumulated through many preceding generations, and is concentrated from many lines of ancestry. Yet the belief is universal that the acquired characters due to food during the growing period have *some* force, and that this force is cumulative in successive generations. All the observed facts in the experience with herds and flocks point in this direction." The breeding of small and delicate Alderney cows was furthered by systematic underfeeding of the calves. Large-sized breeds have originated in regions of abundant food, and smaller breeds in districts of scantier forage. "This can hardly be due to accident." In short, "if these acquired characters are in no degree whatever transmitted, then certain practices of breeders, which are

founded upon the contrary belief, are delusive and expensive mistakes."

We have given this argument at some length, since it deals with a subject of great practical importance, and since it is presented to us with the double authority of Cope and Brewer. It is, however, on every count most disappointingly inconclusive. If the size is a function of four variables,—(*a*) the inheritable constitution of the stock (statistically determinable in certain of its expressions at the beginning of a period of observation); (*b*) the individual modifications produced by altered nutrition (approximately determinable by control experiments and observations); (*c*) the possible occurrence of modification-inheritance; and (*d*) the amount of discriminate selection within a given period (also admitting of more or less precise statement),—then the only feasible way of reaching a conclusion as to the importance of any one factor—say the third in this case—is to eliminate the others one by one.

As to the Alderney cows, it is admitted by all that the skilful breeder can breed small or breed large, either by relying wholly on the selection of a sufficiently variable stock, or by assisting selection by modification kept up for each generation; but this does not touch the question at issue.

And if it be a fact that large-sized races always come from regions of abundant nutrition, and *vice versâ*, it is plainly consistent both with natural and artificial selection.

As to the argument that unless modification-inheritance be a fact the practice of breeders is an expensive mistake, one is tempted to retort that the latter is at least as likely as the former; but the sufficient answer is that breeders, even though they may think they do, never put their stake on the doubtful card.

Finally, it may be noted, though this is a point rather for the biologist than for the breeder, that experiments on increased size of parts are more decisive than those which refer only to the size of the whole.

Manly Miles gives two cases to illustrate what seems to him a general fact, the occurrence of modification-inheritance in breeding: "The fashion of raising lambs by nurses of other breeds, and drying up the dam at once to keep her in show condition, resulted in seriously diminishing the inherited capacity for milk production in the females of the family as treated." "Cows on short pastures and under careless management will form the habit of 'going dry' early in the season, and this habit of giving milk for a short period is not only transmitted, but becomes a marked peculiarity of the females of the family that is persisted in under better conditions of food supply."

But these and numerous similar cases only show, what is universally admitted, that a nutritive disturbance in the mother is apt to affect the nutritive vigour of the offspring.

Brewer (cited by Cope, 1896, p. 436) reports what may be called a good case. Sheep taken from a favourable region to one with alkaline or salt soil, dry climate, and corresponding forage plants, acquire a certain harshness in the wool. The change begins immediately, "but is more marked in the succeeding fleeces than in the first. It is also alleged that the harshness increases with succeeding generations, and that the flocks which have inhabited such regions for several generations produce naturally a harsher wool than did their ancestors, or do the new-comers." Of course, the second generation would naturally have harsher wool than the new-comers, but if harshness really *increases* with succeeding generations, the case is one of the best as yet brought forward.

Immunity.—Another typical line of evidence is based on the study of immunity. To this very important, but very difficult, subject we have referred in another chapter, but the particular point here may be briefly stated. It is well known that some natives are relatively immune to yellow fever; this is now a heritable quality; the question is whether it can be regarded as originally an acquired character. Was it in origin a modification of the bodily metabolism subsequent upon the disease? It seems very difficult to adopt this interpretation, and most authorities incline to the other alternative of regarding immunity as a constitutional variation which has become dominant in the race by the elimination of those members who were not immune.

It may be objected, however, that there are cases where a mother rabbit or guinea-pig has been artificially rendered immune to certain diseases, and has afterwards had young born immune. This may be due to a kind of infection before birth, some anti-toxin or other having probably passed from the mother to the unborn young. (Misunderstanding No. V.)

Medical Arguments.—A medical argument which has convinced many is somewhat as follows. Its cogency rests on the difficulty of drawing hard-and-fast defining lines.

It is alleged that a pregnant woman with smallpox may infect her unborn offspring—a clear case of intra-uterine contagion.

A tubercular mother may have an offspring without tuberculosis, but with something wrong with its heart. Here a constitutional diathesis, stimulated by a bacillus, is followed by a result in the offspring quite different from the condition in the parent.

Toxins produced by bacterial disease in the parent may affect the offspring without inducing any special disease, but by weakening its constitution and power of resistance.

Toxins produced, apart from bacterial disease, by a saturation of the parent with alcohol, opium, and the like, may affect the offspring both functionally and structurally, with the result that there are diseases and malformations.

It has been shown experimentally that toxins (hydrocyanic acid, nicotin, alcohol, etc.) may, directly injected into the eggs of fowls, affect the development so that malformation results. It is stated that the effects of lead-poisoning on the offspring may be wholly due to the father. Therefore it seems legitimate to infer that toxins produced in the body may have a direct effect upon the germinal material.

It is not shown, however, that the effect on the offspring is the same as that induced in the parent—which is the biological point under discussion—and it is a wild hypothesis that an ordinary modification liberates anything comparable to a toxin.

Alcoholism.—Habitual drunkenness in a parent or in the parents produces familiar modifications, and may be followed by dire results in the offspring. But before drawing the hasty conclusion that definite structural results of alcoholic poisoning

on the parent's body are in the strict sense transmitted to the offspring, we do well to consider—(1) that the intemperate habits of the parent may be the expression of an inherited psychopathic disposition, and it is this which is transmitted to the offspring; (2) that the saturation of the body with alcohol may have a direct effect on the nutrition and developmental vigour of the germ-cells; (3) that the children of drunkards often become accustomed to alcohol as part of their food, from the days of suckling onwards.

Nervous Diseases.—Prof. Binswanger of Jena, a famous student of psychiatry, has expressed his inability to find evidence that a mental or nervous disease acquired during the individual life is, as such, or in partial expression, inherited by the offspring. There are, he of course allows, numerous cases in which an inheritance of mental or nervous diseases can be traced from one generation to another; but his difficulty was to find a case where it could be securely maintained that the first occurrence of the disease was due to external influence.

It may, of course, be urged, though it seems an untenable extreme, that mental and nervous diseases never have an exogenous origin, but are always referable to germinal defect. If so, it simply forces us to say that this line of argument is closed as far as the question of the transmissibility of modifications is concerned.

Modifications of Habits and Instincts.—Many animals are very plastic in their habits, and some show some plasticity even in their instincts. It seems an interesting line of experiment to try to determine whether there is any evidence of transmission of peculiar *individually modified* habits. For an expert discussion of the subject we must refer to Principal Lloyd Morgan's *Habit and Instinct*.

There are obviously many difficulties. The experimenter must be sure that the original change of habit is really *modificational*, not an inborn idiosyncrasy. He must be careful to

eliminate the possibility of the offspring learning by imitation or suggestion. He must also exclude the possibility of selection. He must remember that the offspring are probably as docile, as plastic, as adaptable as their parents, or perhaps more so. Mountaineering mules come to have an extraordinary power of adapting themselves to peculiar exercises, but mule does not inherit from mule!

A hen becomes an adept in rearing ducklings: will her own children, put to a similar task, be less fussy than she was at first? House-martins have learned to build beneath the eaves: has there been any hereditary transmission of this acquired habit, or is it merely "the result of intelligent adaptation through the influence of tradition"? Have grouse inherited the habit of flying so as to avoid telegraph wires? Is it indubitably the case that the kittens of a cat "taught to beg for food like a terrier" may spontaneously exhibit the same peculiar habit? These are some of the cases which Lloyd Morgan discusses, and his conclusion is that the evidence for the transmission of acquired habit is insufficient.

§ 10. *As regards Mutilations and the Like*

When we think of the bellicose activities of our ancestors, it seems almost absurd to discuss the question of the transmissibility of the results of mutilations, wounds, and other injuries. Moreover, it is well known that dishorning of cattle, docking of horses' tails, curtailing of sheep, cropping of dogs' ears, and similar practices, have been continued for many generations without any known hereditary effect. The circumcision of the children of Jews and Mohammedans has gone on for many centuries, but there is no demonstrable structural result. Yet the question is one of *possibilities*, and there is a huge literature of observations and experiments.

Few Useful Results.—The net result, it must be confessed, is very disappointing, and the reasons for this are not far to seek.

(1) Many of the experiments and observations have failed to conform to the ordinary canons of scientific method. Many of them overlook the probability of coincidence, identify *post hoc* with *propter hoc*, mix up observation and inference, or base a conclusion on a small number of instances. It may be noted that cases suggesting the transmission of the results of mutilation and injury are most abundant in the older, less critical literature. What may be called good cases have been very scarce of recent years, though many observers have been on the watch for them.

(2) Some of the kinds of experiment—*e.g.* the amputation of large parts or of portions of internal organs, such as the spleen—are evidently of a kind which must be rare in nature. Therefore, though such "fool's experiments," as Darwin would have called them, may have some indirect value, they tend to be of little significance to the evolutionist.

(3) The experimental repetition of those mutilations and injuries which *are* common in nature is of little value, since nature's experiment shows with sufficient clearness that the results are not transmitted. If they were there would be but little now left of man and other combative organisms. As Hartog says, "The tendency to transmit the mutilation itself would be so ruinous as to rapidly extinguish any unhappy race in which it was largely developed" (*Contemp. Rev.*, v. 64, p. 55). As a matter of fact, even in the individual lifetime the results of mutilation are very often repaired by regeneration, which in its specialised expression is probably the adaptive outcome of prolonged selection.

(4) If the results of mutilation can be in any degree transmitted, they must affect the germ-cells in some specific way. The improbability of this is very great in the case of many mutilations, such as lopping off a tail. The amputation has often little demonstrable effect beyond a slight irritation of the tissues at the cut surface; the organism's reaction bears little relation to the actual effect produced; a considerable part of the body has been lost, but there is no constitutional disturbance—the

reaction is a mere scar. Why should one expect the offspring to have a shorter tail because its parent has been curtailed ? Might one not as reasonably expect a longer tail ? No one has ever observed that the descendants of much-pruned fruit-trees or decorative shrubs are any the smaller in consequence. The length of the hair in offspring is not known to be affected by the frequent cropping, clipping, or shearing of their parents. In fact, the structural results of most mutilations are not modifications in the usual sense.

(5) But there are cases in which the removal of a part has deeply saturating effects. Thus the removal of a thyroid gland may have an influence on many parts of the body. In such cases, therefore, the possibility of the germ-cells being influenced is more conceivable. But, unless the change in the offspring—supposing that there is some change—corresponds to the direct change wrought upon the parent, we have not to deal with modification-inheritance of the first degree, which is the only question under dispute.

(6) Since the structural change due to a mutilation is not on the same plane as the ordinary modifications which occur in nature, we do not expect useful results from further mutilation experiments. We may refer, however, to the suggestion made by Dr. J. W. Ballantyne,* that in this connection, as with other modification experiments, investigators err by beginning at too late a stage, after the organism is firmly set. It may be that experiments on early stages would yield more positive results. It may be that the germ-cells in their early generations are more reachable by, or sensitive to, somatic influences.

Illustrations.—In our brief discussion of this well-worn subject, we shall for convenience distinguish three categories : (A) amputations, such as docking the tail ; (B) wounds, such as the rupture of the hymen ; (C) deformations, such as the compression of the

* "Discussion on Heredity in Disease," *Scottish Med. and Surg. Journal*, vi. (1900), p. 312.

Chinese lady's foot. Under each category we shall notice merely a few typical cases, which may be added to as the reader pleases by referring to the literature cited, or by consulting the great work of Delage.

Amputations repeated Generation after Generation.—Circumcision among Jews and Mohammedans, docking horses, dogs, and sheep, cutting off parts of the ears of dogs, dishorning cattle, are cases in point, and there is no evidence of transmitted result. Darwin (1879) does indeed cite Riedel to the effect that a shortened prepuce has been induced among the Mohammedans of Celebes, but Delage notes the inconclusiveness of Riedel's observations. Haeckel (1875) and Leidesdorff (*Wien. med. Wochenschr.* 1877) have also stated that a rudimentary prepuce occurs more frequently in races who practise circumcision, but other statistics do not bear this out. As Ziegler says (1886, p. 27), "There is in this respect no difference between Jews and Christians; among the latter a defective development of the prepuce is as frequent as among the former." See also Roth, *Correspondenz-Blatt f. Schweizer Aerzte,* 1884.

Weismann cut off the tails of mice for nineteen generations, Bos for fifteen, Cope for eleven, Mantegazza and Rosenthal likewise, but in no case was any inherited result observed. An American record of the production of a tail-less race almost certainly illustrates an unscientific use of the imagination.

The tails of fox-terriers are often cut, and pups with short tails are sometimes observed. The following case is representative of a number of records. A fox-terrier, whose tail had been cut, had four pups, one with a full-length tail, one with a rather short tail, and two with quite short tails. But the short tails had the usual tapering vertebræ (D. E. Hutchins, *Nature,* lxx., 1904, p. 6).

Delage cites Tietz (1889) to the effect that kittens with an atrophied tail are *frequent* in the Eiffel, where the peasants habitually curtail their cats—in mistaken kindness, for they believe that there is a worm at the root of the tail which keeps them from catching mice! If abortive tails are unusually common in that district, the fact is of much interest, and Delage does not find sufficient explanation in the suggestion of Dingfelder (1887), that, as the peasants leave short-tailed kittens alone, an inborn variation towards short tails has been allowed to diffuse itself. It is, of course, easy to appeal to an innate tendency to shortening of the tail, but it is curious that the examples should be found so generally among domesticated animals,

like cats and dogs, sheep and horses, which are so often artificially docked.

Amputations not repeated throughout Generations.—These form what we may call the "curtailed cat" type, the point being that a she-cat whose tail has been cut off accidentally or otherwise has been known to bear kittens, some or all of which have tails shorter than the normal. The cogency of such cases is annulled when we remember,—(1) the existence of a Manx and Japanese breed of tail-less cats; (2) the occasional occurrence of tail-less or short-tailed kittens as "sports" in the litters of quite normal parents; and (3) the frequently observed variability of the tail region in many mammals. In all such cases at least two inquiries are imperative: (1) some estimate of the probability of coincidence, since the *post hoc* may be no *propter hoc*, but merely a variation which happens to resemble more or less the result of the mutilation; and (2) an investigation into the pedigree of both parents, since there may be in either or in both an innate tendency towards a shortening of the tail. These inquiries are not usually made.

A number of very interesting cases are given by Delage (1903), and it is difficult to dispose of them except by calling them "mere coincidences." One of my colleagues has told me of a case of a child with a peculiar bare patch among the hair, corresponding to a similar area on the mother's head, where the bareness was due to ringworm. The child's patch was bare save for a narrow streak of short hair, stretching about half way across. The patch was a little in front of the mother's, but was similarly situated above the left ear. What can one say but "coincidence"? Or may one suggest that the ringworm found out a hereditarily weak spot?

Wounds repeated Generation after Generation.—We do not aim at any surgical precision in distinguishing amputations from wounds. Our point is simply that there is a difference between the effect of an amputation which may be almost negative, and the effect of a wound which disturbs the relations of parts. The classification is borne out by the fact that whereas there is not a grain of evidence, so far as we know, to lead one to believe in the inheritance of the results or any results of amputations, except when very important organs are operated upon, the same cannot, at first at least, be said in regard to the effects of wounds.

The typical case here is the rupture of the hymen in the first sexual intercourse—a trivial lesion, perhaps, but one which has

occurred in every generation, and one of which no inherited results are known. Nor are there known results of a kind of circumcision practised by Somalis and others on girls as well as boys. In some races ear-boring, nose-boring, and the like, have been practised by both sexes for many generations; and no inherited result has ever been observed.

Casual Wounds.—Darwin cites the case of a man whose thumbs were badly injured in boyhood, as the result of frost-bite. His oldest daughter (S) had thumbs and thumb-nails like the father's; his third child was similar as to one thumb; two other children were normal. Of the four children of S, the first and the third, both daughters, had deformed thumbs on both hands. The cogency of this case depends on whether there was or was not any previous family tendency to thumb-deformity. It may have been that the frost-bite was really an unimportant incident. Darwin gives another case of a man who, fifteen years before marriage, lost his left eye by suppuration. His two sons had left-sided microphthalmia. Here we have probably to deal with an innate eye-defect in the father.

Bouchut * reports the case of a man of twenty-five who injured his hands and feet by a fall from a scaffold. Of five children only one was normal. His son had one finger on each hand and two toes on each foot. A daughter (M) had two toes on each foot, one finger on the right hand, and two on the left. She married a normal man, and of her four children the oldest was normal, the others like herself.

Cases like the last may seem puzzling to those unaccustomed to deal critically with the facts of inheritance. But in reality they are in most cases merely illustrations of the familiar fallacy of confusing *post hoc* and *propter hoc*, of mixing observation and inference (Ziegler, 1886, p. 26). Bouchut does not say that the children showed the same deformity as their father acquired; he does not tell us about the ancestry of the father and mother, an indispensable fact if a case is to be considered seriously, since inborn malformations are common in some families; finally, the frequency of inborn malformations of the fingers and toes must be borne in mind, and the possibility of coincidence allowed.

Ziegler (1886, pp. 29, 30) discusses a number of cases where defects

* *Nouveaux Éléments de Pathologie générale*, Paris, 1882. Cited by Ziegler, 1886, pp. 3, 4.

in the eye occurred in the offspring of animals whose eyes had been operated on, injured, or infected. But experiments in which the eyes are infected with tubercle or the like are not relevant until all possibility of the offspring being infected is excluded; and as for cases such as those given by Brown-Séquard (1880), where the extirpation of the eye-bulb in the parent was followed in the offspring by the loss of one eye or of both, or by corneal obscuration, it is necessary to compare the results with the statistics as to the frequency of various kinds of innate eye-defects.

Deformations.—We do not know all that we should like to know in regard to the artificially deformed feet of Chinese ladies, but there is no evidence that the long-continued deformation has resulted in *any* hereditary change.

For untold ages the herdsmen in some parts of the Nile valley have artificially deformed the horns of their cattle, making them bend forwards, twist spirally, and so forth; but no effect on offspring has ever been observed (R. Hartmann, *Die Haussäugethiere der Wildländer. Ann. Landwirthsch.*; Berlin, 1864, p. 28).

The Rook's Bill-feathers.—Settegast and others have referred to the bristle-like feathers about the nostrils and the base of the bill in the young rook. They are said to disappear mechanically when the bird begins to bore with its beak in the ground, yet they are always present in the nestling. To cite this as an example of the *non-transmission* of a deformation-effect is probably quite erroneous, for there is no proof that the disappearance is causally connected with burrowing. It is probably a constitutional peculiarity that these feathers should be moulted and not replaced. They disappear even if the rook is not allowed to bore (*see* Oudemans and Haacke, cited by Delage, 1903, p. 223). On the other hand, to start from the fact that the bristles disappear even if there is no boring in the ground, and to cite this as an instance of the transmission of a deformation-effect, is equally fallacious. There is no evidence that it was a deformation-effect to start with.

Some Puzzling Cases.—While the argument based on the apparent transmission of the results of mutilation appears to us very weak, it must be admitted that there are some cases which, if accurately recorded, are puzzling. It is desirable that any fresh cases, similar in nature to those which we propose to illustrate, should be studied carefully and without prejudice. Though they may not prove modification-inheritance, they may lead to interesting results.

Prof. Haeckel * records that a bull on a farm near Jena had its tail squeezed off at the root by the accidental slamming of the byre-door, and that it had thereafter a tail-less progeny. This is very interesting, but we are bound to ask—(1) how often tail-less cattle arise apart from curtailing by the byre-door; (2) whether the bull had any tail-less offspring before it was curtailed; (3) how many tail-less offspring it actually had, and so on. It may be that the answers to these questions would be quite satisfactory, but, to make the case cogent, the questions should have been forestalled.

In 1874 Herr W. Besler, in Emmerich on the Rhine, wrote to Prof. L. Büchner (1882, p. 24) to report the following case. At Döbeln, in Saxony, at Eichler's Hotel there, he saw a young dog apparently bereft of ears and tail. When he remarked that the beast had been far too much cut, he was told that this was not the case, for it and its brother had been born so, out of a litter of four. The mother was normal, the father was an "Affen-Pinscher," whose ears and tail had been cut. The same condition had occurred once in a previous litter. Supposing that this was more than an ostler's yarn, we should have to inquire into the ancestry of the father and mother to see whether inborn shortness of ears and tail had ever manifested itself in the family.

Prof. Büchner also relates that in the autumn of 1873 a building-contractor, K——, in Westphalia, bought a duck whose right "wing-bone" had been broken and had mended in a crooked fashion. Next spring the duck had four ducklings, two of which showed on the right wing, and two on both wings, an extra feathered wing (4-5 in. in length), protruding immovably at an angle of 45° above the otherwise normal wing. But this duplicity, if such it was bore no precise relation to the original injury, and probably was quite unconnected with it.

Büchner gives a number of other instances. Thus Williamson saw dogs in Carolina which had been tail-less for three or four generations, one of the ancestors having lost the tail by accident.† But tail-lessness is also known as a germinal variation.

Bronn ‡ describes the case of a cow which lost one horn by ulceration; it had afterwards three calves which showed on the same side

* *Schöpfungs-Geschichte*, ed. 1870, p. 102.
† Waitz, *Anthropologie der Naturvölker*, i. p. 93.
‡ *Geschichte der Natur*, 1871, p. 96.

of the head no true horn, but a small nucleus of bone hanging to the skin. It may have been that an inborn weakness, which led to the ulceration of the mother-cow's horn, took a slightly different expression in the calves.

Dr. J. W. Ballantyne quotes Kohlwey's experiments on pigeons: "He cut off the posterior (first) digit of the foot, and the mutilated bird got into the habit of turning the fourth digit backwards and using it in perching; he got no descendant of these mutilated birds without a posterior digit, but he got a descendant of one of the pairs with its fourth digit turned backwards like the first. The mutilation was not transmitted, but the physiological adaptation to meet it was." Is it sufficient to regard this simply as a coincident variation?

Some of the best cases are those in which a morbid change was associated with the loss or injury of a particular structure. A cow loses its left horn by suppurative inflammation; it has subsequently three calves in which the left horns were abortive (Thaer, 1812). But it may be that the original loss was due to a weakness of germinal origin.

Prof. W. H. Brewer (1892–3) is responsible for launching a large number of rather unseaworthy instances of modification-inheritance. *Inter alia*, he tells the story of a pure-bred game-cock who lost an eye in a fight, and transmitted his loss. While the wound was very malignant, he was turned into a flock of game-hens of another strain, and "a very large proportion of his progeny had the corresponding eye defective." "The chicks were not blind when hatched, but became so before attaining their full growth. The hens afterwards produced normal chickens with another cock."

A trustworthy correspondent writes: "My great-grandmother had one toe broken at a dance; all her descendants are born with one toe bent double—my grandmother, mother, aunt, sister, and myself." But to this almost typical story what can be said except that congenital variations of the toes are common, and that the accident at the dance had nothing to do with the story?

Of great interest is the statement made by some botanists that some peculiar effects on trees due to mites, ants, etc., are transmitted. Thus Lundström says that the little shelters (acarodomatia) produced on the leaves of lime-trees, etc., by mites, may appear when there are no mites.

But, admitting that there are some puzzling cases, we cannot avoid the general conclusion that as regards mutilations, amputations, wounds, and deformations, the case for the affirmative is not strengthened by further inquiry.

§ 11. *Brown-Séquard's Experiments on Guinea-Pigs*

In recent discussions of modification-inheritance much prominence has been given to the experiments made by Brown-Séquard, Westphal, and others on the apparent transmission of artificially induced epilepsy in guinea-pigs. The reason for this prominence is that the case is not without cogency, and that a record of precise experiments (although of a somewhat ugly character) comes as a relief amid anecdotal evidence. Prof. E. Ray Lankester goes the length of saying (1890, p. 375), "The one fact which the Lamarckians can produce in their favour is the account of experiments by Brown-Séquard, in which he produced epilepsy in guinea-pigs by section of the large nerves or spinal cord, and in the course of which he was led to believe that in a few rare instances the artificially produced epilepsy was transmitted." As the case has been often discussed—*e.g.* by Romanes (1895, vol. ii. chap. iv.)—we shall treat of it briefly.

What the Experiments were.—Through a long series of years (1869–91), Dr. Brown-Séquard, a skilful and ingenious, if somewhat impetuous, physiologist, experimented on many thousands of guinea-pigs. He made a partial section of the spinal cord in the dorsal region, or cut the great sciatic nerve of the leg; he observed that the injury was followed after some weeks by a peculiar morbid state of the nervous system, corresponding in some of its features to epilepsy in man; he allowed these morbid animals to breed, and found that the offspring were frequently decrepit, and that a certain number had a tendency to the so-called epilepsy.

Results of the Experiments.—If it be understood that we have omitted or altered a few difficult technicalities, we may call the following statement Brown-Séquard's summary of his results. The inverted commas are ours:

(1) "Epileptic" symptoms appeared in the offspring of parents who had been rendered "epileptic" by an injury to the spinal cord.

(2) "Epileptic" symptoms appeared in the offspring of parents who had been rendered "epileptic" by section of the sciatic nerve.

(3) An abnormal change in the shape of the ear was observed in the offspring of parents in which a similar change followed a division of the cervical sympathetic nerve.

(4) Partial closure of the eyelids was observed in the offspring of parents in which that state of the eyelids had resulted either from section of the cervical sympathetic nerve, or the removal of the superior cervical ganglion.

(5) An injury to the restiform body (associated with the medulla oblongata) was followed by a protrusion of the eye (exophthalmia), and this reappeared in the offspring sometimes through four generations, even affecting both sides, though the lesion in the parent had only been on one of the corpora restiformia.

(6) An injury to the restiform body near the nib of the calamus was followed by hæmatoma and dry gangrene of the ears, and the same conditions reappeared in the offspring.

(7) After a section of the sciatic nerve, or of the sciatic and crural, some of the guinea-pigs gnawed off two or three of the toes, which had become anæsthetic; in the offspring two or three toes were absent. Sometimes, instead of complete absence of the toes, only a part of one or two or three was missing in the young, although in the parent there was a loss not only of the toes, but of the whole foot (partly eaten off, partly destroyed by inflammation, ulceration, or gangrene).

(8) As effects of an injury to the sciatic nerve, there followed various morbid states of the skin and hair of the neck and the face, and similar alterations in the same parts were observed in the offspring.

When the sciatic nerve had been cut in the parent, the descendants sometimes showed a morbid state of the nerve. There was also a similarity in the successive appearance of the phenomena, described by Brown-Séquard as characteristic of the periods of development and of abatement of the "epilepsy," especially in the appearance of the epileptogenic area and the disappearance of hair around that area whenever the disease showed itself.

Muscular atrophy of the thigh and leg followed section of the sciatic nerve, and this was also observed in the offspring.

After cutting the restiform body one eye suffered deterioration; this was seen in the offspring in one eye, or even in both.

In general, the morbid conditions may affect both sides in the parents and only one in the offspring, or *vice versâ*, or the side affected may be different.

One generation may be skipped, but the duration of transmission was in some cases traced through five or even six generations.

The females seemed better able to transmit morbid states than the males.

As to the frequency of transmission, some inherited result was observed in more than two-thirds of the cases.

Brown-Séquard's results were partly confirmed by his assistants, Westphal (1871) and Dupuy (1890), by Obersteiner (1875), and by Romanes (1895). Dr. Leonard Hill divided the left cervical sympathetic nerve in a male and a female guinea-pig, and thereby produced a droop of the left upper eyelid. Two offspring of this pair exhibited a well-marked droop of the upper eyelid. "This result is a corroboration of the series of Brown-Séquard's experiments on the inheritance of acquired characters."

Facts to be noted, which dispose of a Number of Criticisms.—It is stated that the so-called "epileptic" state may also be induced in the dog by injury to the cerebral cortex, and may, in this case also, reappear in the offspring. If this be so it shows that we have not to deal with a tendency *peculiar* to guinea-pigs.

It is stated that the "epileptic" condition does not occur spontaneously—*i.e.* apart from injury to the nervous system—in guinea-pigs. Therefore the interpretation of the apparent inheritance as being due to a fresh variation which happened by coincidence to resemble the parental state, is inadmissible.

As the tendency to "epileptic" fits (which do not last long) was seen only in the offspring of animals which had been operated on, and was manifested only after appropriate stimulus, especially after irritating an "epileptogenic" zone behind the ear on the same side as the original injury, we must pass by Galton's suggestion (1875) of the possibility of reappearance through imitation. Even if it be allowed that there is a certain infectiousness in "fits," this would not apply to the loss of toes, the diseased state of the ear, the protruding eyes, and so on.

It is stated that the morbid condition of the parents was also induced by bruising the sciatic nerve without cutting the skin, or by striking the animals on the head with a hammer. If this be so it seems to show that the result may occur without any associated microbe influence, and possible infection of the offspring thereby (Weismann's criticism, in part). The hypothesis of microbes does not seem to be supported by any definite facts, but we note that it is not entirely excluded by Ziegler in his review of possible explanations (1886, p. 29).

Brown-Séquard experimented with both males and females, and although he got more striking results with the latter, he did not fail with the former. This seems to lessen the force of the criticism that the offspring were affected during gestation, and therefore not, in the strict sense, hereditarily.

Criticisms.—(1) The original modification was cutting, bruising, or destroying part of the nervous system ; the subsequent result was the "epileptic" state, and the various other diseased conditions mentioned. It need hardly be said that the mutilation or injury inflicted on the parent was never reproduced in the offspring, though the subsequent results sometimes were.

(2) The conditions exhibited by the offspring were very diverse—general feebleness, motor paralysis of the limbs, trophic paralysis resulting in loss of toes, cornea, etc., other nervous and sensory disorders, and in some cases the particular "epileptic" state. In a number of cases the condition of the offspring was so different from that of the parent, that the only common feature was that in both cases there were abnormal neuroses. Romanes, while regarding his results as corroborations of those of Brown-Séquard, admitted that the epileptic condition was only rarely transmitted.

(3) Even numerically there was no small diversity in the results. Thus in one set of experiments (Obersteiner, 1875), out of thirty-two young ones born of "epileptic" parents, only two showed symptoms of "epilepsy" and paralysis, three were paralytic, and eleven were only weak. Romanes did not find that any of the offspring of parents who had eaten their toes off showed, even in six generations, any defect in these parts. Even Brown-Séquard only observed this peculiar "transmission" in about 1 or 2 per cent. of cases.

(4) Prof. Ziegler's criticism is partly based on the allegation that guinea-pigs (as we keep them in captivity) are pathological and nervous animals, very readily thrown into an epileptic state. On

making a slight cut in the skin, on the occasion of a small operation on the neck, Ziegler sent an apparently healthy guinea-pig into a severe epileptic fit. But there seems considerable difference of opinion as to this nervousness of captive guinea-pigs.

(5) It seems to us that the original modification was too violent to afford satisfactory data in connection with the present discussion. No matter how neatly the operations were effected, the partial section of the spinal cord, the cutting of the sciatic or of the cervical sympathetic nerve, the removal of the superior cervical ganglion, the injuring of the restiform body, imply very serious injuries, and it is hard to believe that others were not implied in some of the experiments—*e.g.* on the restiform body. But if a modification is violent it may disturb the whole organism, nutritive * and reproductive † functions alike, and it may naturally lead to abnormality in the offspring. Especially may it lead to general decrepitude, which, it seems to us, was the most frequent result. At the same time this hardly touches the most distinctive feature of the experiments, that sometimes there appeared in the offspring morbid conditions precisely similar to the results of the injury inflicted on the parents. It may be, however, that only particular parts of the body are susceptible to the influence of the original disturbance.

Prof. T. H. Morgan (1903, p. 257) directs attention to the experiments of Charrin, Delamare, and Moussu, which have an interesting bearing on some of Brown-Séquard's results. After the operation of laparotomy on a pregnant rabbit or guinea-pig, the kidney or the liver became diseased, and the offspring showed similar affections. The experimenters suggested that some substance set free from the diseased kidney of the mother affected the kidney of the young in the uterus. "May not, therefore, Brown-Séquard's results be also explained as due to direct transmission from the organs of the parent to the similar organs of the young in the uterus?" But this would not be inheritance in the strict sense. It should be noted, however, that what has been just said does not of course apply to those cases in which Brown-Séquard experimented on the male parent. Charrin maintains on experimental grounds that "cytotoxins" may pass not only from the mother to the fœtus, but from either parent to its germ-cells—ova or spermatozoa (see *Revue générale des Sciences*,

* Dupuy, while confirming Brown-Séquard, laid emphasis on the alterations of nutrition after the experiments.

† Sommer notes a diminution of fertility after the experiments.

Jan. 15, 1896). Moreover, Voisin and Peron have found evidence that in epilepsy a toxin is produced which causes convulsions when injected into animals (see *Archives de Neurologie*, xxiv., 1892, and xxv., 1893, and Voisin's *L'Épilepsie*, Paris, 1897, pp. 125–133). It is thus not a mere speculation to suppose that a toxin was produced in the guinea-pig epilepsy, and that this affected the germ-cells of both sexes. This suggestion is made by Prof. Bergson in his remarkable book *L'Évolution Créatrice* (1907), and he adds to the suggestion the query, May not something of the same sort be true in those cases where acquired peculiarities are transmitted ?

Prof. T. H. Morgan (1903, p. 255) also notes an interesting fact. "While carrying out some experiments in telegony with mice, I found in one litter of mice that when the young came out of the nest they were tail-less. The same thing happened again when the second litter was produced, but this time I made my observations sooner, and examined the young mice immediately after birth. I found that the mother had bitten off, and presumably eaten, the tails of her offspring at the time of birth. Had I been carrying on a series of experiments to see if, when the tails of the parents were cut off, the young inherited the defect, I might have been led into the error of supposing that I had found such a case in these mice. If this idiosyncrasy of the mother had reappeared in any of her descendants, the tails might have disappeared in succeeding generations. This perversion of the maternal instincts is not difficult to understand, when we recall that the female mouse bites off the navel-string of each of her young as they are born, and at the same time eats the after-birth. Her instinct was carried further in this case, and the projecting tail was also removed.

"Is it not possible that something of this sort took place in Brown-Séquard's experiment ? The fact that the adults had eaten off their own feet might be brought forward to indicate the possibility of a perverted instinct in this case also." On the other hand, this interpretation cannot apply to some other results which Brown-Séquard observed.

Sommer's Experiments far from corroborating Brown-Séquard's.— In experiments the results of which were published in 1900, Max Sommer repeated some of those which Brown-Séquard and others had made, but without corroborating them.

The so-called "epilepsy" was induced by cutting the sciatic nerve on one side or on both sides ; the tendency to "fits" occurred some

days or some weeks after the operation; they were brought on by rubbing particular areas of the body (the epileptogenic zones); whether they ever occurred spontaneously remained doubtful, since any friction on the appropriate spots—*e.g.* when the animal scratched itself—served to bring them on. After some months the tendency to the attacks disappeared, and irritation of the appropriate areas was followed by only a slight fit or by none. (This is a noteworthy fact.)

The fertility of the "epileptic" guinea-pigs was lessened.

Twenty-three young ones were reared (a small number compared with those in Brown-Séquard's experiments)—six from two pairs in which the father was "epileptic," six from four pairs in which the mother was "epileptic," and seven from five pairs in which both parents were "epileptic." *In no case did "epilepsy" appear in the offspring.* Even paralysis of one or more of the extremities was not demonstrated, though most carefully looked for.

In the parents there were several defects in the toes or ulcerations of the hind extremities, but *in no case was there reappearance of the defects or ulcerations in the offspring.*

Two of the young were decrepit, and in one there was a clouding of the cornea; but there is no warrant for associating this directly with the "epilepsy" of the parents.

Sommer's conclusion is as follows: "As regards the hereditary transmission of epilepsy in guinea-pigs, or of other accidentally acquired pathological symptoms—*e.g.* defects in the toes—we have obtained an absolutely negative result; we have not been able to confirm the experiments of Brown-Séquard and Obersteiner; and we do not think that these can any longer serve as a support to the doctrine of the inheritance of acquired characters." *

Before leaving the subject of these disagreeable experiments we may be permitted to express our opinion that, altogether apart from convictions as to the ethical limits of scientific inquiry, a sound biology is not likely to gain much from experiments the conditions of which are so utterly different from those occurring in the state of nature. It seems to us that they are entirely

* Sommer also points out that the guinea-pig's "epilepsy" does not correspond to true epilepsy in man, but rather to the so-called reflex epilepsy which follows from peripheral nerve-injuries.

different from experiments on decapitated earthworms, curtailed lizards, crabs with lost limbs, and the like, for there the investigator is in touch with injuries which frequently occur in natural conditions.

The case is certainly a difficult one, but from what we have said it must be evident that it cannot be cited without qualification in support of the thesis that somatic modifications are transmissible. It is illegitimate to conclude, as Debierre does (1897, p 4): "Il est donc incontestable que des caractères acquis artificiellement pendant l'âge adulte de l'animal ou acquis naturellement pendant la vie embryonnaire peuvent être transmis par l'hérédité."

Our general conclusion is that the results of Brown-Séquard's experiments do not strengthen the affirmative position; and that their probable interpretation is that the artificially induced epilepsy liberated a toxin which affected the germ-cells in some cases, the germ-cells and the fœtus in other cases.

§ 12. *Negative Evidence in favour of the Affirmative Answer*

In support of the affirmative answer Herbert Spencer adduced what he called *negative* evidence—namely, those "cases in which traits otherwise inexplicable are explained if the structural effects of use and disuse are transmitted."

(1) First he referred to the co-adaptation of co-operative parts. With the enormous antlers of a stag there is associated a large number of co-adaptations of different parts of the body, and similarly with the giraffe's long neck and the kangaroo's power of leaping. Spencer argued that the co-adaptation of numerous parts cannot have been effected by natural selection; but that it might be effected by the hereditary accumulation of the results of use.

It must be admitted that co-adaptations are difficult to account for in terms of the ordinary selection formula, but it is also difficult to accept the use-inheritance interpretation. We do not really know to what extent deep-seated co-adjustment can be effected by

exercise even in the course of a long time, and the theory requires such data before it can be more than a plausible interpretation, with certain *a priori* difficulties against it.

Another interpretation may be suggested. If an animal suddenly takes to leaping, many individual adjustments to the new exercise may arise; if the animals of successive generations leap yet more freely, they may individually acquire more thorough adjustments Meanwhile there may arise constitutional variations making towards adaptation to the new habit, and under the screen of the individual modifications these may increase from minute beginnings till they acquire selection-value (Mark Baldwin, Lloyd Morgan, and Osborn). Nor should it be forgotten that variations in different parts of the body are often correlated. The subsidiary theory of germinal selection is also helpful. Finally, it is possible that in some of these cases the result was not due to the gradual accumulation of minute variations, but was originated by one of those sudden discontinuous changes which are now called mutations.

(2) Secondly, Spencer dwelt upon the notably diverse powers of tactile discrimination possessed by the human skin, and sought to show that while these could not be interpreted on the hypothesis of natural selection or on the correlated hypothesis of panmixia, they could be interpreted readily if the effects of use were inherited. But the difficulty again is to get secure data. It is uncertain how much of the inequality in tactile sensitiveness is due to individual exercise and experience, though it is certain that tactility in little-used parts can be greatly increased by use. Nor is it certain how much of the apparent unlikeness in tactility is due to unequal distribution of peripheral nerve-endings and how much to specialised application of the power of central perception. As Prof. Lloyd Morgan says: "We do not yet know the limits within which education and practice may refine the application of central powers of discrimination within little-used areas. The facts which Mr. Spencer adduces may be in a large degree due to individual experience, discrimination being continually exercised in the tongue and finger-tips, but seldom on the back or breast. We need a broader basis of assured fact." Nor, it may be added, is the action of selection to be excluded.

(3) Spencer's third set of negative evidences was based on rudimentary organs which, like the hind limbs of the whale, have nearly disappeared. Dwindling by natural selection is here out of the question; and dwindling by panmixia—*i.e.* the diminution of a structure

when natural selection ceases to affect its degree of development—"would be incredible, even were the assumptions of the theory valid." But as a sequence of disuse the change is clearly explained. Prof. Lloyd Morgan replies: "Is there any evidence that a structure really dwindles through disuse in the course of individual life? Let us be sure of this before we accept the argument that vestigial organs afford evidence that this supposed dwindling is inherited. The assertion may be hazarded that, in the individual life, what the evidence shows is that, without due use, an organ does not reach its full functional or structural development. If this be so the question follows: How is the mere absence of full development in the individual converted through heredity into a positive dwindling of the organ in question?" Moreover, the convinced Neo-Darwinian is not in the least prepared to abandon the theory of dwindling in the course of panmixia, especially in the light which Weismann's conception of germinal selection has thrown on this process.

§ 13. *The Logical Position of the Argument*

Before we state what appears to us at present the inevitable conclusion, it may be useful to indicate briefly the logical position of the argument.

Weismann has pointed out that there are two possible methods by which the affirmative position—that modifications are transmissible—might be established. In the first place, there might be actual experimental proof of such transmission; in the second place, there might be a collection of facts which cannot be interpreted without the hypothesis of modification-inheritance.

Experiment.—The experimental method has not been followed as often as might have been expected, and where it has been followed the results are far from conclusive. But it is important to remember that although a few good cases of the inheritance of an acquired character would prove the possibility of such inheritance, hundreds of failures to demonstrate the transmission experimentally do not prove that it is impossible.

The Neo-Lamarckian believes that when new conditions of life

operate in an approximately similar way for many generations, they will produce definite and slowly cumulative effects upon the organisms subjected to them. He is by no means committed to the belief that every change of conditions will produce appreciable hereditary effects in a few generations. The point is not whether modifications are fully and completely transmitted, but whether *any trace* of them may be transmitted. Still less is the Neo-Lamarckian bound to admit that any given change of conditions, more or less arbitrarily selected by any one as being convenient for experimental purposes, will produce recognisable results in the following generation. Thus the fact that most of the experimental results are inconclusive or negative does not disprove the Lamarckian belief.

Interpretation.—As to the second method, that of the interpretation of facts, it cannot be very conclusive either, since both sides have to prove a negative in order to establish their case. The Neo-Lamarckians have to show that the phenomena they adduce as illustrations of modification-inheritance cannot be interpreted as the results of selection operating on germinal variations. In order to do this to the satisfaction of the other side, the Neo-Lamarckians must prove that the characters in question are outside the scope of natural selection, that they are non-utilitarian and not correlated with any useful characters—a manifestly difficult task. The Neo-Darwinians, on the other hand, have to prove that the phenomena in question cannot be the results of modification-inheritance. And this is in most cases impossible. Thus we seem to reach a logical dead-lock.

Cases where the Theory of Modification-Inheritance is inapplicable.—It is true, however, that there are certain characters of certain organisms, in regard to which it may be said with some security that they could not have arisen by the inheritance of acquired characters. Thus many insects and the like have adaptive characters in their cuticular structures—knobs suited for crushing, saws suited for cutting, gimlets suited for boring,

and so on. But these cuticular structures are non-cellular, non-living parts of the external investment of the body; they are made and re-made (after moulting), by the underlying living skin. How then can they be interpreted in terms of modification-inheritance? The matter becomes even more difficult when we consider cases in which the adaptiveness is in the colour or markings of these inert cuticular parts. Weismann has argued that, since there are some adaptive characters which cannot be interpreted in terms of modification-inheritance, this hypothetical factor need not be assumed in attempting to interpret the origin of other adaptations, similar to the former, except that the factor in question is not by the nature of the case apparently excluded from having any connection with them.

But it cannot be said that this application of the "law of parsimony" is altogether successful. It may recoil on those who use it. It might be argued that there are some adaptive characters which cannot be readily interpreted in terms of natural selection (as is implied in the appeal of some Neo-Darwinians to "intra-selection," "germinal selection," and so on), and that therefore natural selection cannot be regarded as a generally acting factor. Moreover, the Neo-Lamarckian is at liberty to reply, that he does not regard the modification-inheritance theory as applicable to all possible cases.

Antecedent Probabilities.—If we turn to the antecedent probabilities of the two beliefs, we find that the assumptions of either side are equally improbable to the other, according to their respective points of view. Thus, the supporters of the negative answer may say that they cannot conceive how a particular local modification of the body can so affect the germ-cells that, when these develop into offspring, the acquired character shall re-appear. The supporters of the affirmative answer may say that they find it impossible to believe in the selectionist interpretation of many of the adaptive characters which make up

an organism, impossible to believe that the little items of improvement which are added generation after generation—say in a cricket's musical instrument—can have had selection-value. There are other difficulties on both sides, and it is likely to remain for a long time a matter of opinion which side has the greater difficulties to face.

A Matter of Fact.—It is plain, however, that what we have to ask is whether interpretations in terms of modification-inheritance have any basis in present-day experience, such as selectionist interpretations have, for instance, in domestication on the one hand and variation-statistics on the other. And our survey seems to indicate that it is very difficult to find any empirical basis whatsoever for the affirmative position.

If modification-inheritance were known to be a fact it would in nowise exclude interpretations in terms of natural selection and other factors, for even the most thorough-going Neo-Lamarckian will hardly maintain that his hypothesis, if verified, would be an all-sufficient ætiological factor, and even the most convinced Neo-Darwinians could not refuse to recognise an additional factor if that were verifiable. There is no need to pit one theory against the other in this fashion; the more factors in evolution that are discovered the better!

The question resolves itself into a matter of fact: Have we any concrete evidence to warrant us believing that definite modifications are ever, as such or in any representative degree, transmitted? It appears to us that we have not. But to say dogmatically that such transmission is impossible is unscientific. In regard to that, the truly scientific position is one of active scepticism (*thätige Skepsis*).

§ 14. *Indirect Importance of Modifications*

Importance of Nurture.—Scepticism as to the transmission of acquired characters does not imply that we under-rate the importance of "nurture." We have seen (1) that an appro-

priate environment is the necessary correlate of a normal inheritance, otherwise the organism cannot realise itself in development; (2) that changes in environment and function may provoke variations in the germ-plasm; (3) that the individual is often very plastic and readily acquires adaptive modifications which may be of great individual importance, and may even preserve the life; (4) that the secondary effects of modifications may, in certain cases, reach and influence the germ-cells; (5) that the state of the maternal constitution is very important in cases where there is an intimate connection between the mother and the unborn young.

Selection and Stimulus.—In two other ways changes in the conditions of life are of great importance: they form part of the mechanism of selection, whereby the relatively less fit variants are quickly or slowly, roughly or gently, eliminated; and they act as a stimulus to the intrinsic self-assertiveness and "endeavour after well-being" which characterise living creatures. We must advance beyond the conventional view that the environment is like a net closing in upon passive victims, which can only escape if they have been fitted by germinal variation (or acquired modification) to pass through some of the meshes; we must recognise as a fact of life, what Lamarck and many others have seen with clearness, that organisms actively assert themselves against this closing net, and by active endeavour (also, of course, a variational character when traced back) may win their way through.

Indirect Importance of Modifications.—But there is another important consideration, which has been stated independently by Profs. Mark Baldwin, Lloyd Morgan, and H. F. Osborn—namely, that adaptive modifications may act as the fostering nurses of germinal variations in the same direction. We have referred to this elsewhere, but it may give greater completeness to our survey if we quote a brief statement of the idea as expounded by Lloyd Morgan (*Habit and Instinct*, 1896, p. 319):

"Persistent modification through many generations, though not transmitted to the germ, nevertheless affords the opportunity for germinal variation of like nature.

"Suppose that a group of plastic organisms is placed under new conditions. Those whose innate plasticity is equal to the occasion are modified and survive. Those whose plasticity is not equal to the occasion are eliminated. . . . Such modification takes place generation after generation, but, as such, is not inherited. . . . But any congenital variations similar in direction to these modifications will tend to support them and to favour the organism in which they occur. Thus will arise a congenital predisposition to the modifications in question.

"The plasticity still continuing, the modifications become yet further adaptive. Thus plastic modification leads, and germinal variation follows; the one paves the way for the other.

"The modification *as such* is not inherited, but is the condition under which congenital variations are favoured and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level."

§ 15. *Practical Considerations*

We have seen that the scientific position in regard to the *transmissibility* of modifications should be one of active scepticism, that there seems to be no convincing evidence in support of the affirmative position, and that there is strong presumption in favour of the negative.

A modification is a definite change in the individual body, due to some change in "nurture." There is no secure evidence that any such individual gain or loss can be transmitted as such, or in any representative degree. How does this affect our estimate of the value of "nurture"? How should the sceptical or negative answer, which we believe to be the scientific one, affect our practice in regard to education, physical culture, amelioration of function, improvement of environment, and so on? Let us give a practical point to what we have already said.

(*a*) Every inheritance requires an appropriate nurture if it is

to realise itself in development. Nurture supplies the liberating stimuli necessary for the full expression of the inheritance. A man's character as well as his physique is a function of "nature" and of "nurture." In the language of the old parable of the talents, what is given must be traded with. A boy may be truly enough a chip of the old block, but how far he shows himself such depends on "nurture." The conditions of nurture determine whether the expression of the inheritance is to be full or partial. It need hardly be said that the strength of an (inherited) individuality may be such that it expresses itself almost in the face of inappropriate nurture. History abounds in instances. As Goethe said, Man is always achieving the impossible. Corot was the son of a successful milliner and a prosperous tradesman, and he was thirty before he left the draper's shop to study nature.

(*b*) Although modifications do not seem to be transmitted as such, or in any representative degree, there is no doubt that they or their secondary results may in some cases affect the offspring. This is especially the case in typical mammals, where there is before birth a prolonged (placental) connection between the mother and the unborn young. In such cases the offspring is for a time almost part of the maternal body, and liable to be affected by modifications thereof—*e.g.* by good or bad nutritive conditions.

There is considerable evidence that the mammalian mother passes on the *surplus* nourishment to the fœtus, and that the size of the offspring in mankind depends very directly on the diet and nutrition of the mother during pregnancy. (See Noel Paton, 1903.)

In other cases, also, it may be that deeply saturating parental modifications, such as the results of alcoholic and other poisoning, affect the germ-cells, and thus the offspring. A disease may saturate the body with toxins and waste-products, and these may provoke prejudicial germinal variations.

(*c*) Though modifications due to changed "nurture" do not seem to be transmissible, they may be re-impressed on each generation. Thus "nurture" becomes not less, but more, important in our eyes.

"Is my grandfather's environment not my heredity?" asks an American author quaintly and pathetically. Well, if not, let us secure for ourselves and for our children those factors in the "grandfather's environment" that made for progressive evolution, and eschew those that tended elsewhere.

> "Was du ererbt von deinen Vätern hast
> Erwerb es, um es zu besitzen."

Are modifications due to changed nurture not, as such, entailed on offspring? Perhaps it is just as well, for we are novices at nurturing even yet! Moreover, the non-transmissibility cuts both ways: if individual modificational gains are not handed on, neither are the losses.

Is the "nature"—the germinal constitution, to wit—all that passes from generation to generation, the capital sum without the results of individual usury; then we are freed, at least, from undue pessimism at the thought of the many harmful functions and environments that disfigure our civilisation. Many detrimental acquired characters are to be seen all around us, but if they are not transmissible, they need not last.

(*d*) The plasticity of the organism admits of definite modifications being re-impressed on successive generations of individuals, and this is the more important when we consider what has been said in the section on "The Indirect Importance of Modifications." They may serve as modificational screens until coincident variations in the same direction can emerge and establish themselves. This also cuts both ways in human societies, where natural selection is interfered with, and where naturally prejudicial deviations from the norm are not necessarily punished by elimination.

(*e*) Of particular importance is the fact that man, in contrast to other creatures, has developed around him an external heritage, a social framework of customs and traditions, of laws and institutions, of literature and art—by which results almost equiva-

lent to the organic transmission of certain kinds of modifications may be brought about.

(*f*) Is there not some result of the long-drawn-out controversy on "the inheritance of acquired characters," if we are thereby freed from indulging in false hopes, but are forced to the conviction that "nurture" is more important than ever? Although what is "acquired" may not be inherited, what is not inherited may be acquired. Thus we are led to direct our energies even more strenuously to the business of re-impressing desirable modifications, and therefore to developing our functions and environments in the direction of progress.

It may be, however, that our methods must change with the change in our expectations. For though we can by modification directly influence the individual, and in some measure even control the expression of his inheritance, it is not through modifications that we can hope directly to influence posterity. Man is a slowly reproducing, slowly varying organism. What is above all precious is the conservation of good stock. No number of veneering modifications—superficial screens of organic defects—can atone for allowing a deterioration of the germinal inheritance to diffuse itself or accumulate. For progress which is really organic—for progress, that is, in our natural inheritance—we must wait, or rather work, patiently. The quest after *Eutopias* and *Eutechnics* must be associated with an enthusiasm for *Eugenics*.

Inheritance of Moral Character.—In the development of "character," much depends upon early nurture, education, and surrounding influences generally, but how the individual reacts to these must largely depend on his inheritance. Truly the individual himself makes his own character, but he does so by his habitual adjustment of his (hereditarily determined) constitution to surrounding influences. Nurture supplies the stimulus for the expression of the moral inheritance, and how far the inheritance can express itself is limited by the nurture-

stimuli available just as surely as the result of nurture is conditioned by the hereditarily-determined nature on which it operates. It may be urged that character, being a product of habitual modes of feeling, thinking, and acting, cannot be spoken of as *inherited,* but bodily character is also a product dependent upon vital experience. It seems to us as idle to deny that some children are "born good" or "born bad," as it is to deny that some children are born strong and others weak, some energetic and others "tired" or "old." It may be difficult to tell how far the apparently hereditary goodness or badness of disposition is due to the nutritive influences of the mother, both before and after birth, and we must leave it to the reader's experience and observation to decide whether we are right or wrong in our opinion that quite apart from maternal nutritive influence there is a genuine inheritance of kindly dispositions, strong sympathy, good-humour, and good-will. The further difficulty that the really organic character may be half-concealed by nurture-effects, or inhibited by the external heritage of custom and tradition, seems less serious, for the selfishness of an acquired altruism is as familiar as honour among thieves.

It is entirely useless to boggle over the difficulty that we are unable to conceive how dispositions for good or ill lie implicit within the protoplasmic unit in which the individual life begins. The fact is undoubted that the initiatives of moral character are in some degree transmissible, though from the nature of the case the influences of education, example, environment, and the like are here more potent than in regard to structural features. We cannot make a silk purse out of a sow's ear, though the plasticity of character under nurture is a fact which gives us all hope. Explain it we cannot, but the transmission of the raw material of character is a fact, and we must still say with Sir Thomas Browne: "Bless not thyself that thou wert born in Athens; but, among thy multiplied acknowledgments, lift up one hand to heaven that thou wert born of honest parents, that modesty,

humility, and veracity *lay in the same egg*, and came into the world with thee."

The study of inheritance leaves a fatalistic impression in many minds, and to some extent this is justified. We cannot get away from our inheritance. As the poet Heine said half bitterly, half laughingly, "A man should be very careful in the selection of his parents." On the other hand, although the organism changes slowly in its heritable organisation, it is very modifiable individually; and this is man's particular secret—to correct his internal organic inheritance by what we may call his external heritage of material and spiritual influences.

CONCLUSION

If there is little or no scientific warrant for our being other than extremely sceptical at present as to the inheritance of acquired characters—or better, the transmission of modifications—this scepticism lends greater importance than ever, on the one hand, to a good "nature," to secure which is the business of careful mating; and, on the other hand, to a good "nurture," to secure which for our children is one of our most obvious and binding duties: the hopefulness of the task resting especially upon the fact that, unlike the beasts that perish, man has a lasting external heritage, capable of endless modification for the better, a heritage of ideas and ideals, embodied in prose and verse, in statue and painting, in cathedral and university, in tradition and convention, and above all in society itself.

CHAPTER VIII

HEREDITY AND DISEASE

"Naturam expellas furca, tamen usque recurbet."—HORACE.

§ 1. *Health and Disease.*
§ 2. *Misunderstandings in regard to the "Inheritance" of Disease.*
§ 3. *Are Acquired Diseases transmissible?*
§ 4. *Can a Disease be transmitted?*
§ 5. *Predispositions to Disease.*
§ 6. *Particular Cases.*
§ 7. *Defects, Multiplicities, Malformations, and other Abnormalities.*
§ 8. *Some Provisional Propositions.*
§ 9. *Immunity.*
§ 10. *Note on Chromosomes in Man.*
§ 11. *Anticipation and Intensification of Disease.*
§ 12. *Practical Considerations.*

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§ 1. *Health and Disease*

What is Disease ?—The distinction between health and disease is relative to an ideal—the maximum efficiency and well-being of the organism under given conditions ; and pathology, the science of deranged function or disturbed metabolism—deranged or disturbed in comparison with what we call "normal"—is, strictly speaking, part of physiology, the science of all vital activity. What we call "normal" in one animal—*e.g.* a bird's mode of excretion—is called "diseased" in another ; what is normal at one

period of life—*e.g.* the breaking down of tissue in a chrysalid—may be a disease at another period; what is normal in one part of the body—*e.g.* proliferation of cells—may be a morbid growth in another region. Disease is a relative concept and does not admit of strict definition.

Our point here is indeed a familiar one, for the tritest of quotations remind us of the kinship between genius and madness, or of the resemblance between the lunatic, the lover, and the poet. As a matter of fact, Ziegler remarks, genius, talent, and mental derangement do sometimes occur in one family. The useful glutinous threads of mucus with which the male stickleback fastens together his nest of seaweed are remarkable renal secretions which, if we did not know their utility, would almost certainly be regarded as the symptoms of a kidney disease. Whether we take the changes in the adult salmon when fasting in freshwater, or the dissolution of the blowfly's maggot as it passes into the pupa state, or the condition of the tadpole as it loses its tail and becomes a miniature frog, or the necrosis at the base of a stag's antlers before they fall off, we have to deal with processes which, though now normal occurrences in the cases cited, would in other cases spell disease.

A great authority puts the point tersely: "Disease is a state of a living organism, a balance of function more unstable than that which we call 'health'; its causes may be imported, or the system may 'rock' from some implicit defect, but the disease itself is a perturbation which contains no elements essentially different from those of health, but elements presented in a different and less useful order" (T. Clifford Allbutt, *System of Medicine*, 1896, vol. i. p. xxxii).

Optimism of Pathology.—It does not seem possible to find any criterion which will serve in all cases to differentiate a new variation making for increased efficiency from another which makes for disease. Experience lends security to the judgment of the physician or the breeder in a large number of

cases, but it is probable, as Virchow has maintained, that some new beginnings which are now—looking backward—regarded as normal steps in progressive evolution would at the outset have been claimed by the pathologist as hints of fresh disease. Leaving microbic and acquired diseases out of account, we may safely say that various processes of hypertrophy and atrophy which are associated with disease in a well-finished organism like man are, as it were, recrudescences of important steps in past evolution. The persistence of germinal activity in a patch of cells may give rise to a tumour, but is it not, as it were, an echo of the power that lower animals have of regenerating lost parts? So it may be that some of the cerebral variations which we call for convenience "nervous diseases" are attempts at progress.

Diseases due to Innate Predispositions and to Acquired Modifications.—From the biologist's point of view diseases are of two sorts: (1) they are abnormal or deranged processes, which have their roots in germinal peculiarities or defects (*variations*, to start with), which express themselves in the body to a greater or less degree according to the conditions of nurture; or (2) they are abnormal or deranged processes which have been directly induced in the body by acquired *modifications*—*i.e.* as the results of unnatural surroundings or habits, including the intrusion of parasites. Often, moreover, an inborn predisposition to some deranged function may be exaggerated by extrinsic stimuli, as in the case of gout,* or when a phthisical tendency is aggravated by the intrusion and multiplication of the tubercle bacillus. That is to say, deranged processes which are primarily due to germinal variation often afford opportunity for equally serious disturbances which must be referred to exogenous modifications. A rheumatic tendency may be fatally aggravated by inappropriate nutrition.

* It is now suggested, however, that gout is due to the toxic effect of some germ or germs.

Disease more Frequent in Man than in Animals.—Diseases occur among wild animals, but, so far as we can judge, they are very rare. They are certainly rare when compared with the frequent diseases of mankind. Why is this ? One reason, probably, is that natural selection has a grip on wild life that man has refused to allow it to have over him. Elimination is keener and the wild race is healthier. Animals born diseased are killed off before they can reproduce. To parasites they adjust themselves, or become immune. Another reason is that wild animals live "more natural" lives, and that the stimuli provoking disease are therefore fewer. A third reason, perhaps, is that man is relatively younger than most wild races, and, therefore, with more idiosyncrasies. Fourthly, it seems that where epidemics occur among wild animals, they are almost invariably due to human interference. (See Ray Lankester's *Kingdom of Man*, 1907, p. 32.)

It should also be recognised that man has created around himself a social heritage which often evolves quickly, hurrying and pressing its creator, who cannot always keep pace with it. This is a frequent condition of mental disorder. More generally, we may venture to say that many human diseases, especially of a nervous sort, seem in part due to the fact that the germ-plasm is not varying quickly enough to keep pace with the changes in environment—physical, biological, psychical, and social. We try to adjust ourselves to these by a panoply of modifications, and this business of adjustment is a strain that provokes disease.

As the physiological and the pathological are really but two aspects of the general problem of vital activity, it is mainly for practical reasons that we have ventured to devote a special chapter to the facts of inheritance in connection with disease. Apart from practical interests, it will be seen that, though the available facts in regard to disease do not lead us to any novel considerations which are not illustrated in normal cases,

they throw some useful side-lights on the general problems of heredity.

§ 2. *Misunderstandings in regard to the "Inheritance" of Disease*

As with the transmissibility of acquired characters, so with the transmissibility of the ills our flesh is heir to, we have to face a number of current misunderstandings, which in many cases obscure the real facts. The long series of transmissible diseased conditions which Prosper Lucas, for instance, gave in 1847, will not pass muster to-day. It includes many cases which are outside the rubric of inheritance altogether. A more critical study, particularly of recent years, has led physicians as well as biologists to define a number of distinctions between real and apparent inheritance. Thus, to take a simple instance, it seems a confusion of thought to speak of the inheritance of any microbic disease.

1. **Reappearance not equivalent to Inheritance.**—The reappearance of a diseased condition in successive generations does not prove that it has been transmitted, or even that it is transmissible. The Alpine plants which Nägeli brought to the botanical garden at Munich were much modified in their new environment, and their descendants were similarly modified. The unusual characters reappeared generation after generation, but experiment showed that the reappearance was not due to inheritance, but was due to the re-impression of similar modifications on each successive crop. So it is with many diseased states which reappear generation after generation, not because they have been transmitted, but because of the persistence of the unhealthy stimuli in function or in environment which originally evoked them. Collier's lung is a modificational result; it reappears in generations of colliers, but there is no warrant for regarding it as heritable.

2. **Pre-natal Infection is not Inheritance.**—Even when a child is born with symptoms or definite expressions of a disease which one or both of its parents exhibited, it does not follow that the disease was part of the inheritance. If the disease is microbic, it is never in the strict sense inherited. It may be acquired by infection through the mother during the fœtal period. This may be illustrated by the rather rare occurrence of congenital tuberculosis and by some cases of congenital syphilis. No one who thinks clearly can maintain that these diseases are in the strict sense heritable.

The unborn offspring may be directly inoculated *in utero* with the germs of certain contagious diseases affecting the mother, and this in spite of the fact that the placenta is a wonderfully perfect filter. "Diseases of the contagious type seem to differ in the facility with which they are transmitted by this means. Thus, in the case of anthrax and tuberculosis, the infection of the fœtus through the mother occurs only very rarely, while we know that in that of syphilis the liability is extreme" (Hamilton, 1900, p. 290). It is said that a fœtus *in utero* may take small-pox from the mother; but this is contagion, not inheritance. Syphilitic symptoms may appear in the new-born—microbes from the father or from the mother have passed into the child; but this is contagion, not inheritance. Some say this is an academic distinction without a difference, but to fail to make the distinction means confusion of thought.

3. **Inheritance of a Predisposition to a Disease is not Inheritance of the Disease.**—In many cases it seems possible and useful to draw a distinction between the inheritance of a definite disease and the inheritance of a constitutional predisposition towards it. Thus, since tuberculosis is a bacterial disease, since relatively few children are born tuberculous, and since the disease attacks very unequally those who are equally exposed to the same external conditions of infection, it seems probable that what is really inherited is a constitutional peculiarity (arising originally as a germinal variation), which expresses

itself, for instance, in "vulnerability of the protective epithelia,"—in fact, in a deteriorated power of resistance to the tubercle bacillus.

In the same way, to take a case provisionally non-bacterial, it seems probable that gout is not, as such, transmissible, but that what is inherited is a constitutional peculiarity (arising originally as a germinal variation), which expresses itself in an altered mode of eliminating nitrogenous waste—a constitutional vice which may be exacerbated by excess of food and alcohol.

4. **Acquired and Innate Abnormal Conditions should be distinguished.**—Closely similar abnormal states of the body may arise in two different ways, and their heritability will differ with the mode of origin. If the abnormal condition is inborn in the strict sense—*i.e.* if it is the expression of a constitutional peculiarity arising originally as a germinal variation—the probability of transmission is often great. But if the abnormal condition has been induced adventitiously by external influences (including food, drink, poisons, etc.), then the probability of transmission is slight. The distinction is a real one, but it is not always readily drawn in actual practice.

Thus the difficulty of distinguishing inborn deafness from exogenous or adventitious deafness—the result, for instance, of various infectious diseases,—may, perhaps, explain a curious peculiarity in E. A. Fay's statistics (3,078 marriages, 6,782 children). The percentage of deaf children in families where both parents were deaf was 8·458, while in families where only one parent was deaf the percentage was *larger*—namely, 9·856. There seems something wrong here, and the explanation may be that there are two quite different phenomena slumped under the title deafness—viz. innate or idiopathic deafness, and acquired or exogenous deafness.

As the case appears instructive, let us pursue it further. Where both parents were believed to be congenitally deaf the percentage of deaf children was 25·931; where one parent was deaf congenitally and the other adventitiously, it was 6·538; where both parents were adventitiously deaf, it was only 2·326. Where one parent was congenitally deaf and the other normal, 11·932 per cent. of the

children were deaf; where one parent was adventitiously deaf and the other normal, the percentage was 2·244. In short, there is no evidence that adventitious deafness is heritable at all.

It may be noted further that Fay's statistics show that deafness among the relatives of the parents increases very markedly the likelihood of there being deaf children; and they also seem to show that consanguineous marriages greatly increase the probability of the inheritance of deafness, or of constitutional conditions, *e.g.* lymphoid exaggeration, such as naturally lead to deafness. This is what would be expected from the fact that an individual inheritance is a mosaic of ancestral contributions.

The position we venture to maintain is expressed in the following sentences:—"As inherited (on the part of the offspring) or transmitted (on the part of the parents), Biology includes only those characters or their physical bases which were contained in the germ-plasm of the parental sex-cells" (Martius, 1905, p. 11). Similarly, Virchow says: "What operates on the germ after the fusion of the sex-nuclei, modifying the embryo, or even inducing an actual deviation in the development, cannot be spoken of as inherited. It belongs to the category of early acquired deviations, which are therefore frequently congenital." This pronouncement is the more remarkable since Virchow believed in the inheritance of acquired characters.

Is the Distinction between Innate Disease and Acquired Disease Practicable?—It is true that the distinction between an "innate" predisposition to a disease and an acquired disease "looks better on paper than by the bedside." This is simply an instance of what we continually find, that the "abstract" theoretical concepts of science are not always readily applicable to the intricacies and subtleties of nature. And yet the distinction is quite legitimate and thoroughly sound and useful in the present state of our knowledge. We cannot object to the utility of abstracting an "organism" from its "environment," although we know that a living

creature is inseparable from surroundings of some sort; and we must not object to the distinction between *innate* (or idiopathic) diseases and *acquired* diseases because we know that the innate disease must have an evocative environmental stimulus, and that an *acquired* disease necessarily involves *some* organismal susceptibility.

What, then, is the distinction? It is the old distinction between a variation and a modification. An innate disease presupposes some germinal variation to start with, some germinal peculiarity to continue with. It is there, whether it finds expression or not. If it does not find any appropriate nurture, it will not express itself in development, but neither will the normal process of thinking find expression without the appropriate liberating stimuli. If an indispensable process, the structural rudiment of which is a component part of the normal inheritance, finds no nurture, the organism of course dies. If a dispensable process, such as an innate disease—the structural rudiment of which is also part of the inheritance—finds no nurture, the organism may of course survive if otherwise normal; but the rudiment of the disease may simply lie latent, and may be expressed in the next generation. Eventually, whether it finds expression or not, it may die away altogether, just as useful variations seem sometimes to disappear. This might be called the *racial* cure of disease.

An *acquired* disease is exogenous, not endogenous, in origin. It arises, apart from any particular innate predisposition, as the direct result of inappropriate nurture (in the widest sense); of unnatural function, over-function, or lack of function; and of intruding parasites—*e.g.* bacteria.

But there are two complications—(1) An acquired disease may operate in an organism which has an innate bias to disease —*e.g.* when a tubercle bacillus infects a phthisical constitution. (2) A diseased condition may be the result of premature or local arrests of development, or of excess of development, or of

disturbance of the time-relations of the developing organism: and this may be due (*a*) to an intrinsic weakness or disproportion in some components of the complex mosaic of inheritance, in which case it is likely to be transmitted; or (*b*) to some disturbance of the nutritive and other conditions during ante-natal life, in which case it is not likely to be transmitted.

To sum up in the words of a well-known pathologist, "the term 'acquired' should be applied only to what arises in the individual life-time—from the period of development onwards —under the influence of external conditions; and never to what arises, as we say, spontaneously—that is, from rudiments already present in the germ" (Ernst Ziegler, 1886, p. 13).

All discussion about "congenital," "pregenital," and "post-genital" heredity or inheritance is writing on the sand—mere verbiage and confusion of thought. The inheritance is the organisation of the fertilised ovum—nothing less, nothing more. That the developing offspring may be infected or poisoned at an earlier or later stage, before birth or after birth, has nothing to do with inheritance. The word "congenital" is properly used to denote what is manifested by the offspring at birth; the "congenital" character may be hereditary—*i.e.* due to the parental germ-cells—or it may have been acquired in ante-natal life. But the word is also used by many to imply an innate constitutional character which is part of the inheritance in contrast to a character which has been adventitiously acquired. Therefore, as far as possible (without undue purism or pedantry), the word should be dropped altogether.

§ 3. *Are Acquired Diseases transmissible?*

It seems certain that diseased conditions may arise from germinal variations appropriately stimulated, as in gout, rheumatism,* obesity, and insanity; it seems equally certain that diseased conditions may be induced from without by peculiarities

* Even if gout and rheumatism (in its acute form) be complicated by the presence of specific microbes, we may regard the microbe as the appropriate stimulus to an idiopathic predisposition.

of function and environment, including, of course, food and drink. Without there being any observable hereditary predisposition, a man may acquire cirrhosis of the liver, neurasthenia, cardiac hypertrophy, and so on through a long list. That a man may be invaded by microbes without being in any way peculiarly susceptible to them, or that he may be poisoned in a score of ways without there being any constitutional weakness to blame, seems certain. But are such acquired diseases in any sense transmissible? It seems to us that the answer should be in the negative, but the general reasons for this answer must be sought in the previous chapter—that dealing with the transmissibility of acquired characters in general.

No one can suppose that microbic diseases acquired by the parent can be transmitted to the offspring, though there may be ante-natal infection, and though the offspring may be prejudiced by the fact that the parents had the disease. If the maternal constitution is seriously affected, it is probable enough that the child may be born weakly, or imperfectly developed, or even poisoned. In other words, the embryo is disadvantageously modified by deficient or abnormal ante-natal nurture. If the parental constitution is seriously affected it is possible that the germ-cells may be likewise affected. This is most likely in the case of the ova with their relatively larger cytoplasm or formative cell-substance. In other words, there may be a transmission of secondary effects of microbic disease. The same will apply to any case where it can be definitely said that the parental body is saturated with poisons or toxins. But to admit this is very different from admitting that a specific modification of the parent's body can be transmitted to the offspring. Yet some who should know better persist in calling this "a distinction without a difference."

Leprosy.—In a leprosy district the children of lepers may exhibit the disease, but this may mean nothing more than that they were exposed to the endemic conditions, whatever they may

be, which cause the disease, or that they caught the contagion, if the disease is contagious, as many believe. "It is quite certain," Mr. Jonathan Hutchinson says, "that the children of lepers, born out of leper districts—in England or the United States, for example—never inherit it."

Gout.—Because gout sometimes sets in after a particular course of diet, some have attempted to regard it as an acquired character, just as Herbert Spencer regarded short-sightedness and a liability to consumption as acquired characters. But there is no warrant for such interpretations. In all three cases we have to do with innate germinal qualities which find various degrees of expression according to the conditions of nurture. There is no reason to believe that the expressions of goutiness in a father can specifically affect the germ-cells in such a fashion that the son *thereby* becomes gouty. Moreover, in many cases the son who becomes gouty was born before his father became gouty. What, then, is meant by the "heritability of gout"? The cases of gout "running in a family" are too numerous to allow us to take refuge in the suggestion that a germinal variation which was expressed as goutiness in the father occurs *de novo* in the offspring. All that can be said at present is that the *predisposition* to gout is an inborn character, which, like any other, may be transmitted. Even if gout turns out to be definitely microbic, the general argument will not be seriously affected.

Albuminuria.—There seems to be such a thing as constitutional albuminuria, and a predisposition to it seems to be heritable. This means that a defect or peculiarity in the filtering apparatus of the kidney arises as a germinal variation, and is handed on from generation to generation. Under conditions which may mean nothing to normal subjects, the inborn peculiarity may find expression in the active disease of albuminuria. As in the case of gout, a constitutional tendency to albuminuria is very transmissible, but the disease must not be called "acquired" simply because particular external conditions of life seem to supply the liberating stimuli which lead to its expression. Where the albuminuria is transitory

and of modificational origin, where it is really an acquired condition, there is no warrant for believing that it is transmissible.

OTHER CASES.—It proves nothing to cite instances of myopia appearing in adolescence and reappearing in the early life of the offspring; of neuroses manifested after an accidental shock in the parent, but patent from the first in the child; of rupture manifesting itself in the parent after an abnormal strain, and occurring without apparently adequate cause in the next generation,—and so on. It is always possible, and indeed reasonable, to answer that we have in such cases to deal with an inherited germinal predisposition.

Cardiac hypertrophy due to over-work is in a sense a diseased condition, though from a wider point of view it may be said that the organism is here, as always, doing its best in the way of adaptive response to novel conditions. But is there any warrant for supposing that cardiac hypertrophy in a father will induce cardiac hypertrophy or even a tendency to it in his son? "Of course, the constitution that made the father liable to hypertrophy would also make the child liable, but this is inheritance of a constitutional (non-acquired) character—a thing no one disputes" (Dr. Leslie Mackenzie, *Scot. Med. Surg. Journ.* vi., 1900, p. 324).

Those who accept the concept of a germ-plasm of unimaginable intricacy, persistent with remarkable dynamic inertia from generation to generation, changing and yet stable, oscillating in parts and yet on the whole "breeding true," will not lightly assume that modifications in the body can bring about a specific change of structure in the germ-plasm. It is *possible* that profound bodily changes, such as some acquired diseases effect, may shake the kaleidoscope and provoke a change to a new position of organic equilibrium; but it does not seem likely. On the other hand, important bodily modifications, *e.g.* serious derangements due to infectious diseases, may effect a change in the vigour (functioning-power, growing-power, developing-power, resisting-power) of particular elements in the inheritance. And this admission is probably enough to cover all the well-authenticated cases of inborn changes in the offspring of parents who had acquired serious diseases.

Nervous Diseases.—In regard to so-called "acquired nervous diseases," I venture to quote again from the late Professor D. J. Hamilton (1900, p. 299): "Have we crucial evidence to show that a mental disease may be excited through external agencies, as, for instance, by the abuse of alcohol in a person free from any ancestral taint, and that this disease so excited can be transmitted through several generations? My own impression is that we have not. . . . So far as I am personally informed, I feel that, in mental derangement, and in excess of perhaps any other form of disease, we have to do with an inherited peculiarity or variation—a variation which may have occurred in a far-back ancestor and lain dormant for many generations, but which inevitably manifests itself under conditions of unusual external stimulation, and which is in no respect bound up etiologically with or necessitated by this stimulus. The substratum which underlies the mental peculiarity is allied to that underlying the predisposition to tuberculosis or gout, and, probably, is referable to a fault in metabolism excited, it may be, by an inherent bias towards degeneration in the nerve-cells of the brain, and this is eminently hereditary."

The general verdict of those experts who admit the validity of the distinction between endogenous germinal variations and exogenous somatic modifications may be thus summed up: (1) externally induced nervous disorders (apart from the results of wounds and wholesale poisoning of the system) are extremely rare in persons free from ancestral taint; (2) hereditary transmission in such cases is quite unproved, if we discount cases where the whole system of the parent (including the germ-cells) is poisoned by alcohol, opium, or the like.

In short, whenever a disease has been acquired, when there is no specific predisposition towards it, when it is in biological terminology *modificational*, it seems unlikely that there will be any *specific hereditary effect* on the offspring. The most that can be admitted is that very virulent *acquired* disease may in

a general way poison or weaken the germ-cells along with the whole body, or that in the case of a mammalian mother the fœtus may be poisoned or weakened through the placental circulation.

It must be noted, however, that many medical authorities do not in the least agree with the position which we have stated. Thus Mr. Jonathan Hutchinson says: "Without venturing to do more than mention the Weismann logomachy, which has recently disturbed the creeds of some biologists, I will take permission to avow my belief that with the sperm and germ supplied by parents there may pass to the offspring tendencies to the reproduction of all that these parents had acquired up to the date of the sexual congress. By the term 'acquired' is meant all that has been received by modification of vital processes, not what has been imposed or taken away by external violence." We must refer to the chapter on the transmissibility of acquired characters for our answer to this opinion.

Experimental Evidence.—It is sometimes said that the famous experiments of Brown-Séquard showed conclusively that artificially induced "guinea-pig epilepsy" is transmissible. But a scrutiny of the case, such as we have given in the previous chapter, leaves us reluctant to base an argument on Brown-Séquard's results.

The only other cases which seem relevant are those which have to do with artificially induced immunity. By injections of serum and the like—the details do not concern us—it is possible to render an organism immune, *e.g.* to diphtheria. Are the offspring thereby rendered hereditarily immune? No case is known where the offspring of an immunised father showed any "anti-bodies" in the blood or any hint of immunity. There is no convincing evidence of transmission of immunity from the male parent.

It is known, however, that the offspring of an artificially immunised mammalian mother (guinea-pig, rabbit, etc.) may exhibit immunity. But this probably means that the "anti-bodies," agglutinins, precipitins, or whatever they may be called, passed viâ the placenta from the maternal to the fœtal blood. *But this has nothing to do with inheritance.*

§ 4. *Can a Disease be transmitted?*

This is not a gratuitous question. Perhaps it is best answered in the negative!

"A disease," says Prof. Martius (1905, p. 14), "is not an entity nor a character, but a *process*—an abnormal process injurious to the organism, which is set a-going by a *causa externa* and runs its course in some part of the body." The process is not transmitted, but the potentiality of it is involved in some peculiarity in the organisation of the germ-plasm. "In the sense in which the word 'inherited' is used by biology, *there are no inherited diseases*." They may be a-going before the offspring is born, but they are not as such inherited.

As the authority quoted says, the objector will doubtless at once bring forward the case of hæmophilia, which is markedly heritable. But hæmophilia is not a disease. Does not the subject get along fairly well until he receives a wound? There may be some weakness in the walls of his blood-vessels which makes them peculiarly vulnerable, there may be some obscure peculiarity in his blood which prevents it coagulating, so that bleeding even from a slight wound may be very persistent. But there is no disease, if we mean by disease an abnormal *process*. What is inherited is a peculiarity of the vascular system; or perhaps we should put it negatively, and say that some part of the normal inheritance (some "determinant," in Weismann's phrase) is absent in those who show hæmophilia.

Some inborn peculiarity of the nervous system, originating as a germinal variation, may under appropriate conditions of stimulus or lack of stimulus manifest itself as a disease, such as some forms of paralysis. Some inborn peculiarity of the muscular system, originating as a germinal variation, may under appropriate conditions of stimulus or lack of stimulus manifest itself as a disease—such as progressive muscular atrophy. Similarly, some inborn peculiarity of the alimentary

tract—a variation not in itself a disease (*e.g.* simple gastric achylia)—may in appropriate conditions give rise to disease. Similarly, phthisis is not as such inherited; what is inherited is a predisposition to caseous degeneration of tissue and allied pathological processes.

Thus, though it may appear pedantic, and though it will probably be misunderstood, we are inclined from the biological standpoint to agree with the authority quoted above, that "*there are no inherited diseases.*"

§ 5. *Predispositions to Disease*

Up to this point we have argued that mere reappearance of a disease does not imply that it is inherited; that infection or poisoning before birth is quite different from inheritance; that microbic diseases should never be spoken of as heritable; that there is no warrant for believing in the transmissibility of acquired diseases; and that, if disease means a *process*, the inheritance of predispositions to disease is a more accurate phrase than the inheritance of disease.

But is not this inherited "predisposition" something "mystical," suggestive of the "horologity" of clocks?

It may be mysterious, but it is not "mystical." We may not be able to picture it or define it, but it is like any other germinal potentiality, except that it happens to be prejudicial to the organism. It implies something out of gear in the protoplasmic machinery.

Physically considered, life depends on an ordered sequence of constructive and disruptive chemical processes, and the organism is from the outset predisposed, let us say "geared," to perform these in a certain routine. But the gearings are from the beginning very delicately adjusted: a slight initial difference may mean a life-long friction; a slight germinal bias may determine the trend of the whole life.

Among the pathological predispositions of major importance

in human life we may mention those which result in abnormal nervous processes, in rheumatism with its many forms, in gout, in obesity, in tendency to stone or gravel, in asthma, and so on. The reappearance of these diseases in varying degrees is certain, but what is really transmitted is the original germinal irregularity of gearing. No one can explain what this irregularity precisely is, but it is a common experience, baffling to the physician, that if it is adroitly checked in its outcrop in one direction it may manifest itself in another. He may cure the disease, but he cannot reconstitute his patient. Hydra-headed, the predisposition will show itself in polymorphic guise.

Some men are immune to certain diseases—*e.g.* to scarlet fever; all men are immune to fowl-cholera and many other animal diseases. This immunity is mysterious, but it is not "mystical." Of recent years we have begun to understand it, to *measure* it. *And "predisposition" is the other side of immunity.*

It is probable that some "predispositions" are much more definite than others. Thus, hæmophilia may be due to a retrogressive variation comparable to albinism; some particular item in the normal inheritance has been suppressed or kept latent. But the predisposition to tuberculosis is probably much less definite, and due to a more general disturbance of the "protoplasmic gearing," which finds multiple expressions both structural and functional.

The predisposition to gout is well known to be hereditary. It is probably what may be called a general constitutional predisposition, involving a derangement of the normal metabolism. For while it perhaps finds its primary expression in peculiarities of the digestive and excretory organs, it may affect practically every tissue in the body. Its expression may be accelerated by luxurious living and laziness, but, given the predisposition, it may manifest itself in those who live very carefully and take plenty of exercise. That is the peculiar hardship of it!

It may seem unsatisfactory to refer the origin of constitutional diseases, such as insanity and obesity, to a germinal predisposition—*i.e.* to the *terra ignota* of the fertilised egg-cell. But no other course is at present open. We are only doing in regard to diseases what we must do in regard to all variations. The little that can be safely said of their causes has already been said in Chapter III. Variability is one of the fundamental properties of the living organism, and the germ-cells are potential organisms. In their relation to the body which is their mortal vehicle, and in their own history, there is ample opportunity for variations to arise, and among these variations we must rank predispositions to disease. In short, such predispositions form part of the puzzle of individuality.

If we take a peculiarity like colour-blindness we know practically nothing in regard to its origin. It is not known to be associated with any structural defect of the eye; it is certainly not acquired; it arises in a certain percentage of the population, usually in males; it is a good example of a germinal variation which is exceedingly heritable. In the same way, passing to disease, we cannot tell what a predisposition to diabetes insipidus precisely means; we know it in its expressions in the body, but its origin is as obscure as that of colour-blindness; it is a germinal variation which is exceedingly heritable.

To illustrate the matter further, we may point out that the inheritance of physiological "idiosyncrasies" which do not express themselves as diseases is well established. Thus, the inability to digest the proteids of eggs and milk may be a heritable "family idiosyncrasy." It seems quite analogous to those idiosyncrasies which under appropriate conditions manifest themselves as diseases. A tendency to excessive "freckling" seems to be hereditary; it implies an inborn imperfection in the skin; under appropriate stimulation it may express itself as Kaposi's disease. Scores of similar cases are well known,

and they seem to throw a useful light on what is usually called "the inheritance of disease."

Inherited and Independent Variations.—It is hardly necessary to point out that the occurrence of a particular predisposition —whether it be to gout, to diabetes, or only to "freckling" —may be interpreted either as the outcome of an inherited germinal variation, or as an independent fresh variation similar to one which occurred in ancestors, just as the occurrence of great musical or mathematical talent may be interpreted either as inherited peculiarity or as fresh variation. The facts seem to show that certain variations have great staying-power throughout generations, and also that nature often repeats herself. Each case must be interpreted in terms of what is known of the lineage.

Inheritance of Secondary Effects of Disease.—In many cases it seems legitimate, perhaps necessary, to suppose that a disease in a parent may have a secondary effect on the germinal material, and may prompt germinal variations which find expression during the development of the offspring as diseases.

In some forms of rheumatism there is what may be called a poisoning—an auto-intoxication—of the living body with its own waste-products—*e.g.* urates; in some forms of bacterial disease, as the popular phrase "blood-poisoning" suggests, the same result is brought about by the waste-products or by-products of the intruding microbes; and it seems certain that an equally thorough poisoning may be brought about by the intemperate use of alcohol, ether, opium, etc. Even water-drinkers may be in certain areas the victims of lead-poisoning, for which they cannot reproach themselves. Experts may differ as to the most accurate way of expressing the facts, but it is certain that a man may thoroughly poison himself, for a time at least, with alcohol, opium, tobacco, or the like. Organ after organ may be injuriously affected; the blood, the urine, even the sweat will tell the tale, as it were in protest; and even

on *a priori* grounds we should expect the reproductive organs —apart as they are in some ways from the everyday life—to be affected by the widespread disturbance of nutritive metabolism.

Weismann has suggested that the oscillations of nutrition in the body prompt variations in the germ-plasm. Diseases may cause profound changes in the nutritive stream, and those particularly constant forms of whirlpool which we call the germ-cells, which repeat themselves and propagate themselves, generation after generation, age after age, may as the results of bodily disease exhibit variations. Stable as the germ-plasm must be supposed to be, we cannot conceive of it as an unrelated entity. We believe that this interpretation covers many of the cases which are called "inheritance of disease."

It must also be remembered that while the chromatin of the nucleus is almost certainly the real vehicle of the hereditary qualities, the germ-cells also include some extra-nuclear cytoplasm which may be affected in a general way by somatic changes. The ovum, in particular, has a relatively large mass of cytoplasm—its general cell-substance—which is the preliminary building-material of the embryo. It is cutting it too fine to say that what affects the cytoplasm of the egg is not part of the inheritance, since that is really hidden in the penetralia of the nucleus. The egg-cell is a unity, an individuality, a miniature organism, and anything in it (except, of course, another living creature—namely, a microbe) is at any rate a close annexe of the hereditary vehicle in the nucleus.

It is experimentally certain that germ-cells are markedly susceptible to toxins of various kinds, such as alcohol, nicotin, and hydrocyanic acid, and that abnormal developments result. Therefore, since many diseases produce toxins in the body, these may affect the germ-cells prejudicially, and thus there may be an inheritance of the secondary effects of disease.

What comes practically to the same thing for the *individual*

offspring, though it is theoretically different, may result if the toxins in the maternal body affect not the ova, but the developing embryo. They may saturate through the placenta and disturb the normal course of development. This would be *an ante-natal modification,* and we should not expect its consequences to extend beyond the immediate offspring, unless the same detrimental conditions persisted in subsequent generations.

Illustrations.—" Assume that the last egg of a fowl dying from tuberculosis is fertile. Weismann would admit—every one would —that the chick is likely not to be full-grown and robust. It will fail of 'nutrition,' of a full capacity for regeneration, and of normal resistiveness to environment (terms which require fuller consideration). It would appear, then, that this chick has an idiopathic [say, innate] susceptibility to all and sundry, or at least to several, diseases. It is mere slackness to call that heredity in disease. It is equally apt to be variation; the chick turning out to be epileptic, or deformed, or liable to cholera. That is all that Weismann contends for. The disease has not bred itself" (Dr. George Wilson, *Scot. Med. Surg. Journ.* vi. 1900, p. 321).

Martius puts this problem. Two brothers have the same medium predisposition to tuberculosis; both take measles. During convalescence one (A) becomes definitely tuberculous as the result of exposure; the other (B) has his predisposition increased but resists tubercle-infection. Both marry normal wives and have children. Now, will the children of A have a worse inheritance than the children of B? There seems no reason to answer in the affirmative, unless it can be shown that the toxins, etc., engendered by the progress of the disease so saturate through the whole system that the germ-cells also are specifically affected and thus have their predisposition exaggerated. This seems very improbable. But it is possible that when a disease goes far the germ-cells may be in a general way prejudicially affected. And if they are rendered in a general way less vigorous, there is some likelihood that the disorganisation of the germinal machinery may go further.

It is interesting to inquire whether, in cured cases of phthisis and the like, the protective substances naturally produced, *e.g.* the 'tulase' of Behring, might not even *lessen* the heritable predisposition of the ovum towards the disease in question.

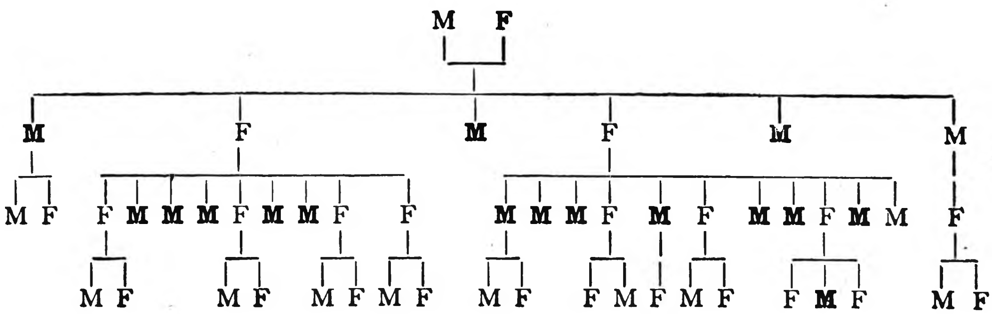
§ 6. *Particular Cases*

Colour-blindness.—This peculiar condition may recur for many generations, but it has an interesting peculiarity. It is usually restricted to the male members, yet a colour-blind man seems never to have a colour-blind son unless the peculiarity was also in his wife's family. Colour-blindness is transmitted from father to grandson through unaffected daughters.

Short-sightedness.—It is generally admitted that short-sightedness is due to an inborn peculiarity in the structure of the eye, occurring in various degrees. In itself it can hardly be called a disease in the strict sense, and conditions of life are conceivable in which it might even be advantageous. The innate peculiarity may become exaggerated and complicated when the eyes are forced to function in a way to which they are ill adapted, and acquired "myopic" modifications may be superadded to what was there by inheritance. Sometimes these may even lead to an actually diseased condition. But though the innate peculiarity may be exaggerated and complicated by the addition of acquired modifications, there is no evidence that these can be transmitted. What is transmitted is a structural peculiarity which began as a germinal variation, and that this is very liable to be transmitted one does not require to go to Germany to see. It is said that short-sightedness occurs, though rarely, among wild races.

Bleeding.—A hæmorrhagic tendency or liability to bleeding is well known to be heritable, but it finds expression only in males. A case given by Klebs and cited by Sir William Turner (1889) is instructive in showing how the tendency, though transmitted through daughters (and therefore part of their inheritance), finds expression only in the males, and in illustrating first a *diffusion*, and then a *waning* of the peculi-

arity. The black letters indicate the affected subjects or "bleeders."



Alcoholism.—There is practical unanimity among physicians that the abuse of alcohol is prejudicial to the race as well as to the individual, but there is considerable difference of opinion as to the theoretical interpretation of the observed facts. As the subject has been very frequently discussed, we shall restrict ourselves to a brief survey.

(1) It is certain that the habit of using large quantities of alcohol is prejudicial to health, "poisons the system," and becomes a pathogenic factor. What constitutes abuse varies, of course, with the individual and his conditions of life. There seems to be little utility in labelling alcohol a "poison," though it is a poison in large doses. Arsenic is a poison to man, yet Gautier seems to prove that the presence of minute quantities of arsenic in various organs of the body is a condition of health. Both as regards arsenic and alcohol, it is the amount and the frequency of the doses that tell.

(2) It is not to be expected that the particular modifications which the parent acquired through abuse of alcohol will be transmitted as such to his offspring. There is no secure evidence of this. The father may acquire cirrhosis of the liver, the child may be epileptic. There seems to be no authentic instance of anything like transmission of cirrhosis of the liver from a drunken father to his son. That a drunken son may also acquire cirrhosis proves nothing.

(3) In interpreting the dismal records of the families of drunken parents it is a mistake to attribute the whole result to the hereditary influence of alcoholism. It is necessary to make allowances for cases in which the offspring "have been in the vineyard too." They may be affected through the mother before and after birth, by becoming early accustomed to doses of alcohol, and obviously by suggestion and imitation, and also by the persistence of the superorganic conditions which "drove the parents to drink." The resultants of these factors may augment the inherited bias or the inherited germinal defect. Where there has been no direct inheritance the nurture-results may simulate the results of transmission.

The Ostiak forces vodka down his child's throat, and the same happens nearer home. "Whisky-babies" occur in Merrie England. But the mischief may begin further back; even before birth the mother may poison her child.

Féré and others have described the disturbing effects which followed injections of small quantities of alcohol into the developing egg of the fowl. Mairet, quoted by Debierre, found that the offspring of an artificially intoxicated bitch by a sound dog showed "alcoholic degeneration" and soon died.

(4) Just as upbringing in an environment of intemperance may bring about results which simulate direct inheritance, so it should, we think, be frankly and responsibly recognised that there is an occupational factor in the persistence of excessive alcoholic habits. From certain occupations—dreary, unwholesome, underpaid, and what not—relief is sought in alcoholic stimulants. As long as these conditions persist they are likely to prompt successive generations to similar expedients, and this must be borne in mind when we try to estimate how much of so-called alcoholic degeneration is strictly speaking due to inheritance.

(5) It is certain that a tendency to intemperance is often associated with other expressions of bodily or mental instability,

but it is difficult to determine whether the alcoholism causes the instability, or whether the instability causes the alcoholism, or whether, as seems most likely, both are expressions of some germinal defect.

Prof. F. W. Mott concludes that "Alcohol is responsible for a *large number of admissions* to asylums." But "how far it acts as the efficient cause of insanity, and how far it is only a co-efficient or coincident in relation to antisocial conduct in an individual potentially insane, rendering such a person certifiable, it is difficult to gauge until more accurate and scientific data are forthcoming" (1911).

And again: "Coincidence and cause may thus be confused, for a lapse from moderation to intemperance may be the first *recognisable* sign of the mental breakdown. Especially is this the case with the involutional psychoses occurring at the climacteric period in women; also men and women between fifty and sixty who suffer from melancholia, and at the same time are the subjects of artero-sclerosis. Again, general paralytics and cases of adolescent insanity may take to drink. There can be no doubt that neurasthenics, hysterics, epileptics, imbeciles, degenerates, eccentrics, and potential lunatics—all those, indeed, with an inherent narrow margin of highest control—possess a marked intolerance to the effects of alcohol, and the failure to discriminate between what is the *result* of alcoholism and what is innate and *due to inheritance* has been the cause of much confusion" (1911). And again this authority sums up, "Alcohol is a powerful coefficient, but not of itself the main cause, in the production of insanity, except in the rather infrequent cases of alcoholic dementia."

(6) It is certain that parental alcoholism and instability (taking the two together) are often associated with alcoholism and degeneracy in the offspring, but this may depend on the inheritance of a "general controlling determinant" responsible for both alcoholism and instability. It is difficult to prove that

parental alcoholism considered, if that be possible, by itself has a hereditary influence on the offspring.

Many facts point to the conclusion that what the intemperate member of an intemperate lineage inherits is the weakness which led the parent to become alcoholic. It does not matter whether we call this a lack of will-power or a neuropathic or psychopathic tendency. It is a heritable constitutional defect, as is clearly illustrated in cases where the parent did not acquire the alcoholic habit until after he had ceased having children. Let us quote two great authorities. Dr. T. S. Clouston observes, "It was not the craving for alcohol that was inherited, but a general psychopathic constitution in which the alcoholic stimulus is an undue stimulus, and the mental control deficient." Prof. F. W. Mott writes, "An inherited weak will-power and lack of moral sense may be transmitted, whereby the individual is more susceptible to temptation and imitation, and in this way environment plays an all-important part."

(7) Dr. Archdall Reid has elaborated with great ability the interesting thesis that alcoholism promotes temperance. The most temperate races are those that have been habituated to the use of alcohol for the longest time, during which those who have an abnormal tendency to intemperance or an abnormal susceptibility to alcohol have been weeded out, leaving a more controlled and more resistent stock. He points out how intemperate families rapidly work themselves out.

(8) In this connection reference should be made to a very interesting point raised by Prof. F. W. Mott, How is it that a chronic alcoholic often has offspring mentally and physically sound? It is probable that we have here an instance of the stability of the germ-plasm in spite of even violent environmental assaults. It is probable also that we have to distinguish between men who become alcoholic through deep-seated constitutional defect and those who have not this excuse. What Mott says is this: "The question is wrapped up in the causes which lead a man or woman

to drink, and my observations and adduced facts seem to show that a man who can drink continually for numbers of years, and keep out of a lunatic asylum, a prison, or a hospital, must have possessed an inherent stable mental organisation, and he in a measure transmits this, the virility of the stock remaining potent in spite of the ruinous habit he has acquired, although it is probable that his offspring would have been stronger and fitter had he been a temperate man. Drunkenness in successive generations would, I believe, undoubtedly lower the virility, and mental and physical degeneracy of the stock would result" (1911).

(9) It is certain that abuse of alcohol is prejudicial to the race by lessening in more ways than one the nutritive capacity of mothers. Thus, to refer to one aspect only, the conclusion of Prof. G. von Bunge's investigation of over 2,000 families is that the increasing incapacity of mothers to nurse their children is referable to chronic alcoholic poisoning continued for generations (*Die zunehmende Unfähigkeit der Frauen, ihre Kinder zu stillen*, 5th edition, Munich, 1907).

(10) The predisposition which facilitated the hyper-alcoholic habit in the parent is transmitted. There may be intra-uterine intoxication of the unborn child if the mother is a drunkard. The tradition in favour of the abuse of alcohol may persist. The conditions of nurture may also tend to induce the alcoholic habit in the offspring; but *there is more.* Much evidence points to the conclusion that the germ-cells may (in cases of extreme alcoholism) be prejudicially affected along with the body of the victim. As it is often only the father who is alcoholic, it follows that the poisoning influence, whether of the alcohol itself or of by-products resulting from the nutritive disturbances which its abuse provokes, may effect the germ-cells as such. "This direct deterioration of the germ is a pathogenic factor of the first rank" (Martius, 1905, p. 23). For if the germ-cells are affected the offspring will also be affected.

(11) There is some experimental and some general physio-

logical evidence that alcoholic poisoning may prejudicially affect the germ-cells, but it is more difficult than most people think to substantiate this from human cases. Thus in the case of intemperate mothers we have to allow for the deranged nutrition as well as for the poisoning, and for the poisoning of the embryo through the placenta as well as for a possible direct deterioration of the germ.

(12) There is some evidence that deterioration in the offspring, as marked by epilepsy, some forms of insanity, lack of control, feeble-mindedness, deaf-mutism and stunted growth, is apt to be intensified and to appear earlier if the parents are alcoholic.

Nervous Diseases.—That the nervous system is particularly liable to disease is well known, and various reasons have been assigned for this. (1) Nervous organs are of all organs the most intricate in their complexity, and nerve-cells are the most highly differentiated cells. But a high degree of complexity involves greater instability, greater liability to accident. A free-wheel bicycle with two or three grades of gearing is a finer mechanism than, let us say, the old-fashioned high bicycle, where even the complexity of a chain was avoided; but there is in the increased excellence the inevitable disadvantage of a greater range of possibility "for something going wrong." (2) Nervous organs have a very limited power of regeneration after injury. There is no increase in the number of our nerve-cells after we are born, and reports of cases of regeneration of nerve-cells after injury are few and far between as regards backboned animals. (3) Characters of recent origin tend to be more unstable than those of ancient date, and the differentiation of man's brain is relatively recent compared with that of his food-canal. Prof. Adami (1901, p. 1319) refers to the discovery made by James Ross of Manchester that "when there is progressive atrophy of the cells in the cortex of the brain, the first motor-cells to show signs of that atrophy are those governing the muscles which differentiate man from other

animals—namely, the opponens muscles of the hand." (4) Hamilton suggests, *inter alia* (1900, p. 298), that the "germ-track followed in the ontogeny of the nerve-cells is very short, far shorter than in the case of many other cells throughout the body, and hence a state of maturity is reached at a comparatively early period, with an inclination to premature decay." (5) It may also be noted that, especially as regards his nervous system, the so-called civilised man takes liberties of unnatural function and unnatural environment, which often tax the plasticity of protoplasm beyond the limits of endurance, marvellously wide as these are, and allow inborn weaknesses to find dire expression. For these and other reasons, then, the nervous system of man is peculiarly liable to disease.

Weaknesses, abnormal peculiarities, and actual diseases of the nervous system are not only very common, but they appear to be peculiarly persistent in family histories. In old days it was often remarked that generation after generation of a particular family might be "possessed of the devil"; and there were families of "sorcerers" and "witches" who turned their hereditary neuroses to account. So now we speak of the neuropathic family.

It is generally admitted that lack of control, morbid idiosyncrasies, subjection to delusions, monomania, hysteria, epilepsy, chorea, locomotor ataxy, extreme passionateness, homicidal and suicidal mania, insanity and imbecility, tend to reappear generation after generation with appalling regularity. It is often said that about one-fourth of those who are confined in lunatic asylums have had some more or less insane not-remote ancestor.

In regard to this very difficult question we wish simply to make three remarks: (1) in many cases what the facts suggest is the inheritance of a general, not a specific, predisposition; (2) on the other hand, there are some instances of apparently very precise and specific inheritance, as if some very definite

"blot on the brain" was transmitted from generation to generation; and (3) that there seems to be little warrant for believing in the transmission of a nervous disorder of exogenous origin.

(1) In most cases the facts seem to suggest that what is inherited and transmitted is a general predisposition to some dislocation or derangement of the nervous system. If such a dislocation or derangement occur in a case where we can exclude the probability of its being due to any infection, intoxication, or lesion of external origin, we must refer it to some initial defect or disturbance in the organisation of the germ. As such, it is likely enough to be transmitted, whether it be hysteria or epilepsy, melancholia or idiocy; but it does not by any means follow that it must be transmitted, or that, if transmitted, it will have in the offspring the form it took in the parent. In fact, the frequency with which the expression changes almost forces us to conclude that what is inherited is something general, not specific. Another reason for this conclusion is to be found in the fact that the nervous disorder is so often associated with some more general constitutional disturbance. Thus the association of hysteria, epilepsy, chorea, etc., with rheumatism is well known. In such cases it is probably more accurate to speak of the inheritance of a constitutional vice, a derangement of metabolism, and to avoid expressions which suggest that there is, to begin with, anything definitely wrong with the cerebral machinery. In the third place, it is instructive to note that the cerebral equipment may work well for years of ordinary life, and yet break down hopelessly in face of some extraordinary excitement or some constitutional crisis (puberty, parturition, menopause, etc.), which again suggests the inheritance of general weakness rather than the inheritance of specific disease.

The fact that predispositions to nervous diseases so often change in particular expression from generation to generation

points to the position which many hold, which is well argued for by Rohde (1895), that what is really inherited is a constitutional peculiarity (arising originally as a germinal variation) which may express itself in general neurasthenia, easy exhaustibility, deficient control, etc., *or*—under sufficient provocation—in some specific form of acute neurosis. After a careful survey Rohde concludes that the only nervous disorders which are transmissible are those which have a germinal origin; and another authority, Dr. T. S. Clouston, says, "A neurotic heredity is seen to resolve itself into general morbid tendencies rather than direct proclivities to special diseases." What is inherited is a predisposition, not a disease; and, fortunately, the predisposition may never realise itself.

What we have just said does not imply that persistent nerve-fatigue and neurasthenia in parents may not favour the outcrop of neurosis in the offspring, for the abnormal nervous condition in the parent may, through nutritive disturbances, affect the germ-plasm in a generally deleterious way (as Weismann expressly says), and the development of the nervous system of the unborn child may be affected disadvantageously by the abnormal condition of an over-fatigued mother.

It is exceedingly probable that many neuroses are due to primary defects in the development of some of the nerve-centres or of the cells that compose these. Thus, a weakening in the developmental power of certain rudiments in the inheritance, which might well arise as a germinal variation, and which might by hypothesis be inherited, would account for the recurrence of certain forms of nervous disease generation after generation, *e.g.* for a similar breakdown at adolescence or in senescence.

(2) On the other hand, there are some cases—a small minority—which suggest that a specific predisposition may be heritable. Thus, some of the records of inherited nervous disorders disclose an appalling exactness in their mode of expression, though it is probable that this is due in part to

suggestion. The point may be illustrated with reference to suicidal mania.

Debierre (1897, p. 19) cites a case, reported by Maccabruni, of a suicide's family. Out of seven, three made away with themselves; a fourth, who was assassinated, left a child who committed suicide. But the tragedy of the inheritance of a suicidal tendency is increased by the fact that it may manifest itself in the offspring at precisely the same age and in precisely the same way as it did in the parent.

"A monomaniac in the prime of life, Moreau de Tours reports, was seized with melancholia and drowned himself; his son, in good health, rich, the father of two well-endowed children, drowned himself at the same age." In another case a man who had met with a disappointment tried to drown himself, was rescued, but afterwards accomplished his design. It was found that his father and one of his brothers had committed suicide at the same age and in the same manner.

It should, we think, be borne in mind that the outcrop of a morbid hereditary tendency at the same age—often a critical age—in father, son, and grandson, may not be any more mysterious than that they should begin to shave at the same age. Nor should we exaggerate the tragedy of similar suicides by forgetting that the methods available are not very numerous. Originality is as rare in suicide as in other actions. Thirdly, we should remember the dire influence of suggestion: secret brooding over the nature of the father's death has doubtless in many cases added weight to the hereditary burden.

(3) In regard to the transmissibility of nervous disorders of exogenous origin—*i.e.* traceable to some external shock or wound—it may be enough to quote the deliberate conclusion of an expert pathologist: "I can find no facts which prove that an acquired disorder of the nervous system can be transmitted to the offspring" (E. Ziegler, 1886, p. 30). Where a nervous breakdown followed a shock, a wound, or an illness such as pneumonia,

and reappeared in the offspring, it is probable that there was behind the provocative stimulus an inborn predisposition, and that the latter alone is transmitted. The case of alcoholism has been discussed separately.

Microbic Diseases.—In the strict sense there can be no inheritance of microbic diseases, for a microbe cannot form part of the organisation of the germ-plasm. "No specific infective disease is hereditary, if we use the term 'heredity' in the sense which Darwin and the biologists have given to it. If it appear congenitally it is simply communicated to the fœtus by infection" (A. A. Kanthack, in Allbutt's *System of Medicine*, vol. i. p. 555). Let us take two concrete cases—tuberculosis and syphilis.

Tuberculosis.—As this familiar disease, in its many forms, is always associated with the presence of a specific microbe, the tubercle bacillus, it is not in itself transmissible. What is transmitted is a predisposition making infection easy, a vulnerability of epithelial surfaces, a weakness in the power of resisting and dealing with the invading microbes. As Debierre puts it, "On ne naît pas tuberculeux, on naît tuberculisable."

Theoretically, it matters little when or where infection occurs, but the various possibilities are of practical interest.

(1) It seems very unlikely that the spermatozoon is ever the bearer of the tubercle bacillus. Out of sixteen guinea-pigs inoculated with the sperm of tubercular males, six became tubercular, according to Landouzy and Martin, but many have repeated this experiment with negative results. Landouzy, quoted by Debierre, gives the case of a phthisical officer who married a wife without any hereditary taint in that direction. The five children all died of tubercular disease; but, of course, this may have been due to post-natal infection.

(2) Similarly, it seems very unlikely that the ovum is ever the bearer of the tubercle bacillus.

(3) In a few cases there is direct evidence that the mother may infect her unborn offspring, the bacillus passing through the placenta. In rabbits and guinea-pigs and some other animals this ante-natal infection has been demonstrated; but it is interesting to notice that while tuberculosis is extremely common in cows (sometimes,

it is said, in 16 per cent.), the young calf is very rarely tubercular. Leclerc found only five cases out of 400,000. As to man, only about a dozen instances of congenital tuberculosis were admitted by an expert as securely established in 1905, and Dr. R. Schlüter's exceedingly careful scrutiny (1905) of alleged cases of congenital tubercle in human infants led him to the conclusion that for practical purposes the possibility of ante-natal infection might be in this case disregarded. Thus, Prof. D. J. Hamilton writes: "With extremely few exceptions—so few that they may almost be neglected—children are not born tubercular even of tubercular mothers, nor are the young of animals born tubercular under like conditions" (1900, p. 293). Even if the mother have genital tuberculosis, specific contamination of the unborn child seems rare, and there is no proof that genital tuberculosis in the father has any specific effect on his offspring.

(4) In all ordinary cases, then, the infection with tubercle bacillus occurs after birth, and in many cases long after.

The fact that tubercular disease may be a shadow over a family history for generations is doubtless mainly due to an inheritance of what began as a truly germinal or blastogenic variation, which is only a biological way of expressing what the physician means by "a particular predisposition," "a tubercular temperament," "a diathesis," and so on. To discuss what the particular weakness precisely is does not fall within our province; Prof. Hamilton says, "Most likely the particular vulnerability resides in the epithelial protective coverings of the body being too little resistant, too easily stimulated by external agencies, too readily penetrated by the parasite of the disease" (1900, p. 294). "In support of this assertion are to be taken into account certain epithelial manifestations which accompany the tubercular habit—namely, the very dark or very light degree of colour of the hair, the overgrowth of hair in the bushy eyebrows and long eyelashes, and, lastly, the occurrence of a lanugo-like overgrowth in tubercular children along the spine and over the legs. To my mind, these all point to an anomaly of the epithelial type which is peculiar to the tubercular habit of body" (Hamilton, 1900, p. 295).

If it be the case that the tubercle bacillus usually gains access, even to the lungs, mainly by the digestive tract, and almost entirely through the intestine, and may penetrate into the large lymph channels without any apparent lesion, we have still perhaps to do

with epithelial vulnerability, and in any case, which is all that our argument requires, with a general constitutional peculiarity or germinal variation.

For the benefit of those who are not satisfied with referring the hereditary predisposition to a germinal variation (though beyond this vagueness it is hardly safe at present for any biologist to venture), we wish to quote again from the late Prof. Hamilton's address on "Heredity in Disease," which marked a distinct step in the discussion of the subject.

"Where has the inherited strain come from? What is its ancestral history? Can it be generated by vicious surroundings? I question whether it can. No doubt, once in the blood, the particular habit may be fostered by every external agent which tends to deteriorate the natural powers of resistance. But will such external agencies tend to produce a particular colour of hair, a certain narrowness of chest, tallness of stature, and other peculiarities which are distinctive of the tubercular constitution? My conviction is that they will not, and that we must go much further back in the history of the human race to get at the explanation of the matter. My own impression is that these features are the lineal descendants of a variation which took place far back in our history, that the variation has occurred irrespective of surroundings or external agencies, and that its influence has been propagated in the descendants ever since. It may be a variation which is common to many races, but one which apparently is intensely hereditary" (1900, pp. 295–6). It should be noted, however, that this way of looking at the facts is not unanimously accepted. Some experts will hardly admit the inheritance of even the tubercular diathesis as a thing more to be remarked than the disposition to typhoid or diphtheria. The tubercle bacillus is very parasitic, and may bide its time for years, slowly producing, even from a single infected gland, all the appearances of the tubercular type. Moreover it should be remembered that (*a*) open-air animals rarely suffer from tuberculosis, but suffer at once when confined; (*b*) that well-to-do, well-nourished people are much less liable than the poor and ill-fed; and (*c*) that phthisis is commonest where overcrowding is greatest, and lessens as hygiene improves.

In any case, the distinction between the inheritance of a predisposition to a disease and the inheritance of the disease is far from being a quibble about words, as some prejudiced writers still declare.

This is evident from the successful results of modern preventive medical practice in regard to consumption.

Statistics showing that in one sanatorium 35 per cent. of the tubercular cases belonged to tubercular families, in another 38 per cent., and so on, are not of great theoretical interest. The reappearance is due, in the first place, to the inheritance of the constitutional predisposition—*i.e.* of a bodily soil very open to the entrance of the weed, very suitable for its culture, very weak in the power of resisting its ravaging growth. The reappearance is due in the second place to the too common persistence of functional and environmental conditions favourable both to infection and to the enfeeblement which means defeat. It is enough to allude to the lack of fresh air and exercise. It is an old story, told in many forms and very true, that one boy of a tubercular family went to sea and alone escaped the doom which befell his brothers and sisters. Nor are cases unknown where a return in imagined security to the old home in the town, and to the sedentary life of a clerk, has resulted in belated but fatal infection. In the third place, we have to bear in mind the likelihood of one member of a family infecting another with the tubercle bacillus.

But besides the transmission of a constitutional vulnerability, besides the rare occurrence of ante-natal infection, besides the likelihood of household infection, besides the persistence of conditions of life which favour the disease—are there any other factors? There are probably two others. On the one hand, a seriously tubercular mother may be unable adequately to nourish her offspring before and after birth, and the ill-nourished offspring becomes the more readily the prey of disease. On the other hand, it seems likely that the bodily disturbances induced by tubercular disease in the parents may prejudicially affect the vigour of the germ-cells themselves, and thus lead to the production of inferior offspring.

Syphilis.—As this disease appears to be due to a specific microbe, its reappearance in the offspring of syphilitic parents is not strictly a fact of inheritance. The father may infect his offspring without the mother being affected, and it is possible that the microbe may enter the ovum with the spermatozoon. The father may affect his offspring indirectly by first infecting the mother—that is, the microbe may pass through the placenta into the child. In certain cases—*e.g.* when conception occurs soon after the date of the primary disease—the probabilities of the offspring being infected are great.

though there is always some uncertainty. Of twins, one may be infected and the other not. But the chances are so many that a patently syphilitic father will have syphilitic or in some way deteriorated children, that the marriage of a patently syphilitic subject can only be called a crime—the more heinous since the disease in the offspring is often more serious than in the parent. It seems, furthermore, certain in the case of this disease that, apart from the specific ante-natal infection of offspring, the toxins produced by the microbes in the body of the parent or parents may induce general disturbance or debility of constitution in the germ-cells, and thus result in inferior offspring.

§ 7. *Defects, Multiplicities, Malformations, and other Abnormalities*

For convenience, though we are here passing away from disease, we may include in this chapter a few references to the inheritance of abnormalities in the wide sense.

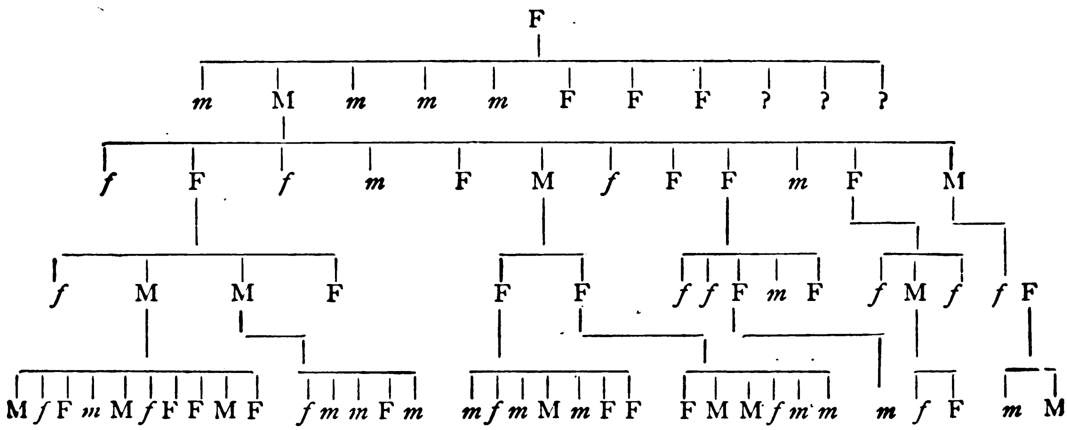
(A) **Defects.**—There are many cases on record where an absence or deficiency of a particular structure has persisted for several generations. Some of these minus variations have been utilised by man as the origin of new domesticated breeds. It is enough to mention hornless cattle—*e.g.* Polled Angus; earless sheep—*e.g.* of Syria and China; tail-less cats—*e.g.* of Japan and the Isle of Man; short-tailed dogs and pigs. Such cases must be distinguished from others quite different in nature, where a part is absent through mechanical constriction during development, and then, of course, no inheritance is to be looked for.

Albinism or absence of pigment is frequently inherited in man.

Sir William Turner gives a rather striking case where a shortening or imperfect growth of the metacarpal bone of the ring-finger of the left hand "was traceable throughout six generations, and perhaps even in a seventh, and was, as a rule, transmitted alternately from the males to the females of the family."

In a family in Pennsylvania described by Farabee many of the

members had all their fingers and toes two-jointed like the thumb and big toe. The normal members had normal children, even in the case of a first-cousin marriage. The abnormal members married normal individuals, and the fourteen families bred in this way contained 33 normals and 36 abnormals—a close approach to equality. The abnormals are indicated by capitals.



Along with defects of parts we may include imperfections due to an arrest of the normal course of development at certain stages, perhaps through inadequacy of nutrition, perhaps because of what we must vaguely call "deficient developmental vigour." Thus, hare-lip is practically the persistence of a normally transient condition, and cleft palate is in the same category. Hutchinson has recorded hare-lip in ten members of a family of twenty.

Inhibitions or disturbances during ante-natal life are believed to result in various other abnormalities, such as cleft-palate, cervical fistulæ (persistence of traces of visceral clefts), spina bifida, certain peculiarities of the eyes and teeth, and so on. These abnormalities occasionally recur repeatedly in a family tree, but it seems probable that what is really inherited is a deficiency in "developmental vigour," accentuated by nutritive defects on the part of the mothers during the period of gestation.

(B) **Multiplicities.**—As with defects, so in regard to multiplicities. Polydactylism has been known to recur through six

generations of a human family. Bédart records quadruple polydactylism of hands and feet through three generations of a Périgord family (*C. R. Soc. Biol. Paris*, 9th series, vol. iv. 1892, p. 367). Lucas cites a case of a Spanish family which included forty instances of polydactylism, and Pliny tells of similarly distinguished families in ancient Rome. Hereditary polydactylism is well known in cats.

(c) **Malformations of Parts.**—There are records showing the hereditary recurrence of abnormalities in dentition, in the eyes,

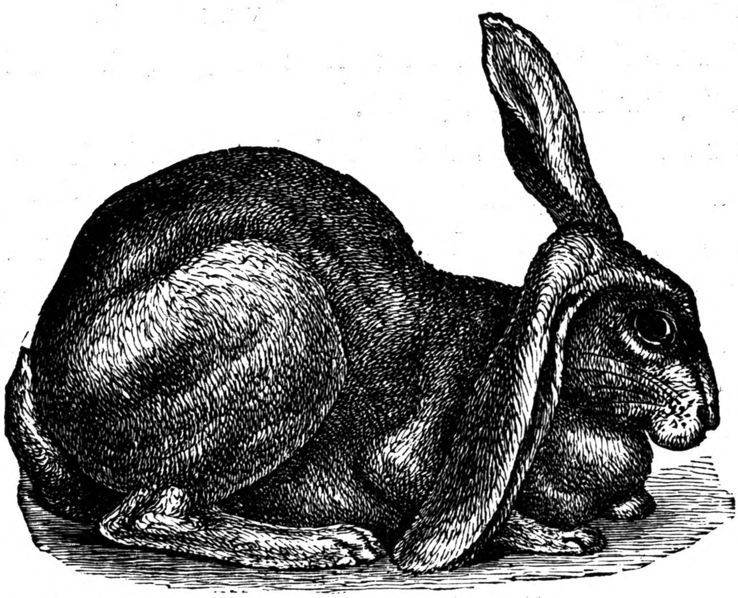


Fig. 28.—Half-lop rabbit, an abnormal variation, which by artificial selection has become a stable breed. (From Darwin.)

in the hands (*e.g.* webbed fingers), in the feet (*e.g.* club-foot)—indeed, in most parts of the body; but in most cases the likelihood of transmission does not seem to be great.

(d) **Pre-natal Influences resulting in Mutilations, Multiplications, etc.**—Recent embryological experiments have shown incontestably that certain types of monstrosity can be readily induced artificially by subjecting the developing ovum to shakings, alterations of temperature, injections of various stuffs, and so on; and although the experiments relate mainly to birds,

amphibians, fishes, and lower animals, there is some evidence that analogous factors may occasionally operate in mammals. Thus, the pressure of amniotic strands may divide the rudiment of a limb into two or may cause a mutilation. All such cases are equivalent to accidents in after-life; they are in no way expressions of the inheritance, and there is no evidence to show that they have any effect upon the inheritance.

"The Hapsburg lower lip or the large nose of Orleans is truly an item in the inheritance, but the occasional absence of an arm (due to a constriction of the rudiment by a strand of the amnion) is an intra-uterine acquisition; it is congenital, but it is not inherited" (Martius, 1905, p. 14).

It has sometimes been remarked that certain families show a hereditary tendency to have wens ("small cystic or encysted tumours") on the head and upper parts of the body. The nature of the growth, its inconstant position, and the time at which it appears (usually about middle age) show that we should not speak of the inheritance of a wen, but rather of the inheritance of some skin-weakness.

§ 8. *Some Provisional Propositions*

1. Abnormal Peculiarities may find Expression in One Sex only.—(*a*) Most of man's defects and predispositions to disease are transmitted to both sexes (equally or unequally) through successive generations. Polydactylism and some forms of cataract, Huntingdon's chorea and diabetes insipidus, may be given as instances. The liability of the sexes is in some cases very unequal; thus exophthalmic goitre is rare in males.

(*b*) In some other cases, such as albinism, there is a marked tendency to skip a generation or even two generations, but as in the first group both sexes are liable to be affected. Albinism is well known to be a recessive character, and we can readily understand, as Mott points out, how the marriage of two apparently

quite normal individuals, *e.g.* cousins, each having albinism latent or recessive in the germ-plasm, may result in one or more of the offspring being albinos (*Medical Chronicle*, 1911, p. 75).

(*c*) In a third group the disease finds expression in one sex only (the males), but may be transmitted by the apparently unaffected other sex. Thus hæmophilia—a chronic liability to excessive bleeding—is almost always, if not (according to Bulloch and Fildes) always, confined to males. It is partly associated with weakness in the walls of the blood-vessels, and partly with a lack of coagulating power in the blood. The disease passes from an affected father through an unaffected daughter to a grandson. For some unknown physiological reason it does not find expression in the female sex, unless, perhaps, in some disguised form.

Colour-blindness or Daltonism has been recorded (Horner) through the males only of seven generations, and it is usually confined to males. Déjérine cites a pedigree (*fide* Appenzeller) in which all the males had a kind of cataract through four generations. Mott mentions as other cases of abnormal conditions generally restricted to the males, " pseudo-hypertrophic paralysis " and " hereditary optic neuritis or optic atrophy."

Edward Lambert, born in 1717, is said to have been covered with " spines." His six children showed the same peculiarity, which began to be manifest from the sixth to the ninth month after birth. One of his children grew up and handed on the peculiarity to another generation. Indeed, it is said to have persisted for five generations, and in the males only,—*unilateral transmission.* (See *Phil. Trans.* 1755 ; Prichard, *History of Mankind*, 1851.)

2. The Expression of Disease-inheritance may change from Generation to Generation.—" Diseased organisms are apt to breed disease, but not always, though sometimes, their own disease." This cautious statement seems to be well borne out by the facts.

Hannot (*Arch. gén. de Médecine*, 1895) gives the following illustrations. A typical gouty subject, with his joints hampered by accumulations of urates, may beget a son as gouty as himself,

or it may be that the son is asthmatic. An alcoholic patient may have an epileptic child. A tubercular mother may have a child with Pott's disease. A man infected with syphilis may have a son afflicted with general paralysis. In regard to the last case, it may be, as has been recently suggested, that even general paralysis has its associated micro-organism, which finds a suitable soil in syphilised tissues. It is probable, at all events that syphilis is one of the predisposing causes of general paralysis.

It is easy to add to these illustrations. "An inheritance from a parent who has suffered from psoriasis may possibly be transmitted as ichthyosis, or some form of chronic eczema or lichen" (Hutchinson, 1896, p. 66). A man with tabes may beget a child with epilepsy. An eye defect, such as microphthalmia, may be represented in the offspring by quite a different abnormality. Perhaps the best examples of change of outcrop are furnished by nervous disorders. Convulsions in one generation may be represented by hysteria in the next, or hyperæsthesia by mania, or insanity by epilepsy, and so on.

As Prof. F. W. Mott says, speaking from a wide knowledge of nervous diseases: "It is not necessarily insanity that is inherited, but a neuropathic tendency in the stock which manifests itself in many forms, *e.g.* epilepsy, asthma, migraine, chorea, diabetes, exophthalmic goitre, neurasthenia, eccentricity, hysteria, criminality, fanaticism, suicide, genius of a certain type, and insanity" (1911, p. 80).

It may appear for a moment that these illustrations prove too much, suggesting as they do that the inheritance of morbid predispositions is very inconstant. But it must be noted, first, that there are even more abundant instances of diseased predispositions breeding true, and second, that they bear out what has been already emphasised, that in most cases what is inherited is rather an abnormal metabolism than a specific disease.

It is doubtful whether we are warranted in speaking of the "transmutation of disease," for this phrase seems to suggest that a particular kind of process may change in hereditary transport into another

particular kind of process. It is probable that some diseased conditions which get different names are fundamentally the same; it is their expression only that changes in response to the conditions of nurture and environment.

The facts of what is often called "transmutation of disease" suggest that what is inherited is sometimes a very general peculiarity, which finds this or that expression in relation to the conditions of the body—a very variable soil—and according to the liberating stimuli which are available, such as the diet, climate, and other conditions of life.

It is well known in medicine that a predisposition or diathesis may express itself in half a dozen different ways—being polymorphic, as it is said—though there may be one way or two ways which, being most frequent, may be called "diagnostic" or "distinctive." Thus, the tubercular tendency has several different ways of expressing itself, probably depending mainly on the nature of the nutritive and other environmental influences.

But if the same disease may find different expression in, let us say, three brothers, it is not surprising that the disease of a parent may take a different, though analogous, form in the offspring, and perhaps a third form in the grandchildren. It may be intensified, or weakened, or directed on new lines, the change depending, so far as we can see, partly on the amphimixis or duality of the inheritance, and partly on the external conditions. Thus, if both parents have a markedly phthisical tendency, the probability is that there will be in the offspring a more pronounced similar predisposition than if one of the parents had belonged to an untainted stock; or, again, apart from amphimixis, a thorough change in habits and surroundings may at least greatly inhibit the phthisical outcrop in the offspring.

There is probably a very simple reason why a hereditary tendency to nervous disease should have different expressions in successive generations, and it is this: that many if not most abnormal neuroses—*e.g.* epilepsy and insanity—emerge during

the period of development, and are due to defects or arrests in the development, ultimately traceable to deficient nutrition of the tissues, or to a lack of vigour in the germinal material to begin with. What is inherited is this general tendency to debility, and it is for the environmental influences to determine the precise lines of least resistance.

3. **Some Predispositions to Disease are much more heritable than others.**—Statistics seem to prove what a general outlook suggests, that some predispositions to disease are much more likely to have hereditary re-expression than others. But the cautious student will bear in mind two saving clauses: (1) that non-expression does not necessarily imply non-inheritance, for a morbid character often skips a generation, or more than one; and (2) that recurrence does not necessarily imply inheritance, for a particular predisposition may crop up *de novo*, or, in other words, the fountain of variation may repeat itself. No one will go the length of supposing that the rheumatic tendency has not originated afresh over and over again, or of tracing the whole burden of rheumatic disease back to man's pre-human ancestry because rheumatism occurs in monkeys. As already noted, acute rheumatism is probably microbic.

A few illustrations of the variable probabilities of transmission must suffice. In one long family history, gout is said to have persisted for four centuries. Out of 523 gouty subjects, 309 had a family taint (about 60 %); out of 156 cases, 140 had a family taint (about 90 %); various sets of cases show percentages varying from 50 to 100. Out of 104 cases of diabetes mellitus, 22 had a family taint (about 20 %). In one long family history, dealing with about 400 members, there were 26 cases of hæmophilia; in another, dealing with 100 members, there were 17 "bleeders."

Out of 901 admissions to an asylum, 477 had insane relatives; out of 321 cases of epilepsy, 105 had a family taint (about 35 %); out of 208 cases of hysteria, 165 had a family taint (about 80 %).

Various specialists on mental disorders have found reason to believe in hereditary transmission in from 25 to 85 per cent. of their patients, the diversity being doubtless in part due to the great variety of nervous diseases.

4. **Many Uncertainties in Inheritance.**—It is seldom possible to say that a predisposition to a disease expressed in a parent *must* be transmitted to the offspring. A predisposition to a disease is rarely a sharp and definite character, such as we are familiar with in "varieties" (of a species), which so frequently breed true. It often means simply a slight disturbance of what we may call the "gearing" of an organism—a slight derangement of the normal sequences of the metabolism. It is an unstable fluctuating variation. It is usually admitted that there are families hereditarily predestined to be gouty or rheumatic, but is any expert on either disease willing to stake his reputation on the prediction that a particular gouty father is sure to have gouty children?

It is not difficult to understand why individual prediction as to the inheritance of predispositions to certain diseases is impossible. An individual inheritance is a mosaic of parental and ancestral contributions. The reduction of these in the process of maturation, the possibilities of fresh permutations and combinations in amphimixis, the variability of the germ-plasm under the influence of nutritive oscillations in the blood-stream, the probable occurrence of some sort of intra-germinal struggle among the hereditary items (all living and self-assertive), the importance of nurture in favouring the expression of one character and hindering that of another—the whole circumstances of the case, in short, are so complex that prediction for individuals is out of the question, no matter how certain we may be as to the average result in 1,000 cases. A predisposition to a disease has to run the gauntlet just like a predisposition to mathematical insight or musical talent. There is just this difference, that predispositions to disease are commoner, that they often occur

in many ancestors of a given child, and that the chances of their being transmitted are therefore greater.

Even when there is reason to believe that an offspring has inherited a predisposition to a particular disease, it does not necessarily follow that this item in the inheritance must be expressed in development.

5. **Predispositions may dwindle away.**—There is, at least, some evidence to show that hereditary tendencies to particular diseases may dwindle until it becomes almost permissible to say that they have been eradicated.

The biological interpretation of this is twofold: (1) that interbreeding with an untainted stock may result in an overpowering of the vicious tendency or in a re-habilitation of the normal; and (2) that in the course of selection the more severely tainted tend to die out, thus leaving the race relatively stronger. The biological caution is that we must not infer from non-reappearance, or from non-expression—*e.g.* in healthier conditions of function and environment—that the evil tendency has ceased to be inherited. Prof. Hamilton says (1900, p. 301), "My firm conviction is that if a vicious line be introduced it may die out, and probably does in most cases die out by interbreeding with a series of pure stocks; but that no reliance can be placed upon its not recurring atavistically, it may be, generations after."

§ 9. *Immunity*

Immunity to a disease may be inborn or acquired. It may be acquired in various ways: by having the disease and surviving it—thus, recovery from smallpox usually confers an immunity which lasts for years; by being inoculated with the modified virus of the disease—thus, vaccination confers immunity from small-pox; by being inoculated with a very minute quantity of the virus; by being inoculated with the metabolic products or toxins of the microbes; by having injections of the blood or

serum of another artificially immunised organism; and even by ingesting the microbes or their products. (See A. A. Kanthack, Allbutt's *System of Medicine*, vol. i., article "Infection.")

It seems that artificial immunity depends on processes within the body which make the tissues able to destroy intruding bacteria and to rob their products of their fatal potency. It seems that specific anti-toxins are formed which immunise the body to specific infection.

An acquired specific immunity may be transferred from a mother to her offspring through the placenta, but this is not in the strict sense inheritance. Ehrlich and others have shown experimentally that rabbits and the like may be born immune if the mother has been artificially rendered immune; and it has been asserted that in mankind the fœtus may become, through the mother, immune to smallpox.

In support of the view that those who are infected with a plague and survive can transmit relative immunity to their offspring, attention is called to the fact that epidemics have their day and cease to be. But this admits of another interpretation—the plague eliminates the most susceptible and leaves the race in this way more resistent. What is transmitted is the inborn power of resistance—which may be enhanced by the selective process, especially if the plague is very severe and lasts a long time. It is to be feared that there is very little evidence of the transmission of *acquired* immunity—to smallpox, for instance!

What is to be made of the alleged fact that two of the commonest infective diseases in Britain—namely, scarlet fever and measles—are much less virulent than they used to be? According to a skilful pathologist, Dr. William Russell, "this is almost certainly to be attributed, not to an attenuation of the virus, or to improved treatment, but to a measure of immunity acquired by a population whose progenitors for generations have passed through the ordeal of these infections."

Of course, this is a very difficult question, in regard to which no one would wish to dogmatise. But one must not too readily assume that the correct interpretation is the hereditary transmission of acquired immunity. (1) It is possible that the micro-organisms concerned are evolving in the direction of attenuated virulence. (2) Much may be due to improved treatment. Thus "measles" may not be really milder, but simply better treated. (3) The result may be in part due to an elimination of the most susceptible, which leaves the race as a whole more resistent. (4) There may be a quite independent widespread variational change in the direction of more resisting power to these two diseases—a germinal variational change quite apart from the ordeal of infection. (5) The power of resistance may be improved by diet; thus measles is often most acute in out-of-work winters, and least acute when the nutritive conditions are good. (6) The severe so-called "types" of certain diseases were probably "mixed infections." Nowadays there is perhaps a greater number of "pure infections." (7) Some of the more virulent germs are probably being stamped out. There is no proof that the germ of the now somewhat rare scarlatina maligna is the same race as that of the common scarlatina simplex. (8) It is possible that the mothers may through the placenta confer their own acquired immunity on their offspring.

Natural immunity is a well-known inborn peculiarity, sometimes racial, sometimes personal, and manifested in various degrees. Negroes are relatively immune to yellow fever and ague; Algerian sheep are relatively immune to anthrax; certain individuals appear to enjoy peculiar immunity in the midst of epidemics.

It is generally believed that racial immunity has been gradually wrought out in the course of natural selection. Germinal variations in the direction of immunity enable their possessors to survive; the survivors transmit their refractory constitution; the

most susceptible are persistently weeded out: and thus, if the infection persists long enough as a common mode of elimination, a race may become relatively immune. No one doubts the heritability of natural immunity, though there is still great uncertainty as to what the mechanism of immunity is.

§ 10. *Note on Chromosomes in Man*

In a very interesting paper (1906), H. E. Ziegler has illustrated the modern doctrine of the material basis of inheritance with particular reference to man. He takes the number of chromosomes in man as 24 (see page 46); but the argument is not affected by the particular *number*.

Let us take two parents, P^1 ♂ and P^1 ♀; in each body-cell there are 24 chromosomes, and in each mature germ-cell there are 12 chromosomes. Thus the fertilised ovum has again 24, and in each cell of the offspring (F^1) there are 12 chromosomes of paternal origin (from P^1 ♂) and 12 of maternal origin (from P^1 ♀).

In the mature sperm-cell or egg-cell of the parent (P^1 ♂ or P^1 ♀) there are 12 chromosomes, but it does not necessarily follow that 6 of these must be from a grandfather (P^2 ♂), and 6 from a grandmother (P^2 ♀). Why not? Simply because in the reduction of chromosomes from 24 to 12, which occurs in maturation, it does not necessarily follow that the parental (P^2) contributions are retained in equal number. The total number 12 always results, but it may be made up of 5 from P^2 ♂ and 7 from P^2 ♀, or of 8 from P^2 ♂ and 4 from P^2 ♀, and so on. Suppose the mature sperm-cell had 9 from P^2 ♂ and 3 from P^2 ♀, then, as far as the paternal inheritance goes, we should expect the offspring (F^1) to be very like its grandfather.

The chances are that the grand-paternal and grand-maternal contributions in any mature germ-cell will approximate to equality, but the numerous possibilities enable us to see one reason at least why there is often great diversity in a family

If we suppose that the chromosomes are all of equal value, there is always a theoretical possibility in a human family of 169 different combinations of the grandparental contributions. It is a well-known fact that certain predispositions to disease may be seen in two or three children in a household and be quite absent from other two or three.

The chromosomes of the four grandparents (P^2) are made up of contributions from eight great-grandparents (P^3), and if the reduction processes were always quite regular, the 24 chromosomes in a fertilised egg-cell should contain in the 12 of paternal origin, 6 grand-paternal and 6 grand-maternal; and either of these groups of six should contain 3 great-grand-paternal and 3 great-grand-maternal contributions. But if the reduction-processes do not exhibit this improbable regularity, we may look for a great variety of possible mosaic arrangements,—as indeed we find. If we accept the chromosome theory, we can readily understand how an innate defect or morbid predisposition in, let us say, a grandfather, may be sifted out of the lineage; and similarly for a virtue!

The business becomes more complicated when we notice that in a number of cases there are differences in the size of the individual chromosomes; it may be that particular characters are bound up with particular chromosomes, and are not represented even by analogous items in others. Thus a particular predisposition to disease in a particular organ may be embodied in a particular chromosome, which might be thus conceivably sifted out of the lineage altogether. In man, however, the chromosomes are approximately of equal size.

Ziegler supposes that in man each chromosome has the same value and influence, that each is capable of influencing the whole organism, and that they differ only inasmuch as they are derived from different ancestors, and thus embody diverse hereditary tendencies.

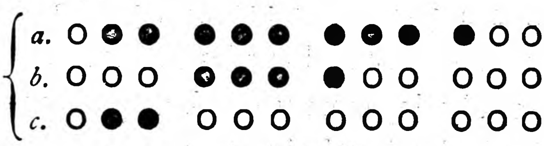
The chromosomes of an individual usually represent eight

families, and it is therefore likely that every one has some chromosomes with a predisposition to some disease, such as phthisis, or gout, or diabetes, or "nerves." A mosaic made up of contributions from eight families can hardly avoid some such taint. But the important point, Prof. Ziegler continues, is this,—what numerical proportion do the tainted chromosomes bear to the untainted? If 3 out of the 24 have a diabetic taint, this will mean much less than if there were 12 tainted. It follows that taint on both sides of the house is particularly dangerous.

Ziegler gives the following illustrative schema.

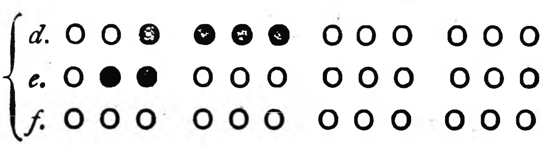
Father—with marked taint, inherited from his father and mother, as shown by the dark chromosomes—13 out of 24.

Three mature sperm-cells showing three different combinations



Mother—normal, though with a latent taint, inherited from her mother, as shown by the dark chromosomes—4 out of 24.

Three mature egg-cells showing three different combinations



It is evident that the child resulting from $a \times d$ would have a badly tainted inheritance, that another resulting from $c \times f$ would have a good inheritance, and that another from $c \times e$ would be in the same position as the mother, and so on.

The practical importance of this very theoretical inquiry is great, for we have here a suggestion of the way in which taints may fall out of a lineage. A tainted determinant may be literally lost in the course of the reducing divisions of the germ-cells

or it may be counteracted in amphimixis by stronger healthy determinants from the other germ-cell.

§ 11. *Anticipation and Intensification in Disease*

Careful work in recent years has brought into prominence a very interesting and important tendency in certain diseased conditions. The unsoundness becomes in successive generations *intensified and antedated.* This has been called "the law of anticipation." According to Nettleship, anticipation in hereditary disease means the manifestation of the morbid change at an earlier age in each successor, either in members of each succeeding generation as a whole or in successively born children of one parentage.

Thus a particular morbidity like the diabetic tendency may come on earlier and earlier in successive generations. Thus, too, a mentally degenerate stock may show earlier and earlier collapse, *e.g.* by lack of resisting power to tubercle.

As to the theory of this anticipation, various suggestions have been made. Dr. Nettleship says: "Anticipation or antedating of onset or of completion in a family might be taken to show the transmission of an acquired character. But it may probably be explained as well or better by assuming certain defects, taints, or vices of the system, say of the blood, are not only hereditary in the true or germinal sense, but able to produce toxic agents in the embryo which have an evil influence upon all its cells, and thus so lower their power of resistance that the innate hereditary factor has freer play and is likely to manifest itself earlier. There may also be toxic agents in the embryo that have no relation to the hereditary vice but yet may and probably do act in a similar manner as excitants of the disease." That is to say, more roughly, a general and progressive degeneracy may give a specific morbidity more and earlier opportunity.

Another authority who has done much to disclose the facts of

"anticipation," Prof. F. W. Mott, looks at the problem in another way. He supposes that unsound determinants in the germ-cells may be attracted to one another, "and as it were coalesce or crystallise out," thus causing the disease to appear in a more intense form and at an earlier age.

In the present state of our knowledge it is impossible to be otherwise than vague in regard to these things. It may be useful, however, to recall Weismann's subtle conception of the struggle of determinants within the germ-plasm, which he supposes may account for alleged cases of definite variation in a given direction. Perhaps this "anticipation" is of the nature of a definite variation, though as it happens in a fatal direction—a *facilis descensus Averni.*

But the practical importance of the fact of anticipation is obvious. It is one of Nature's many devices to eliminate unfitness, to sift out the unsound members of the stock. The diseased condition is pushed further and further back, even to birth, or even before it!

§ 12. *Practical Considerations*

A medical authority (quoted by F. Martius, 1905) goes the length of saying, "For the practitioner the concept of heredity is quite useless, and he should not deal with it at all. What is wrought out during the life of the individual can be dealt with. *What is due to the parents is unalterable.*"

This is an extreme expression of the practical pessimism which many feel. We cannot choose our parents; we cannot refuse our legacy.

But this extreme pessimism is unwarranted. The fact is that, if "the inheritance of disease" really occurred to the extent and *in the manner* many medical writers assume with so much conviction, the human race would have been extinct long ago, or in any case we could not now have the broad and strong stream of

healthfulness which, in spite of all disease, still surges around us.

Let us look for a little at the more hopeful aspects of the question:

(1) As regards microbic diseases, a *predisposition* to which may be inherited, the progress of hygiene and preventive medicine tends increasingly to diminish the risks of infection or of fatal infection.

(2) There is some reason to believe that, in regard to some microbic diseases, a relative constitutional immunity is in process of evolution.

(3) There is no scientific warrant for believing that acquired diseases—*i.e.* those arising as modifications from without, to which there is no specific predisposition—are as such transmissible. By liberating toxins and the like in the body, or by depressing the general nutrition, acquired diseases *may* prejudicially affect the germ-cells, and therefore the offspring. But this is more remediable than specific changes in the germ-plasm.

Our view of the harm done by an ill-considered widespread belief in the transmissibility of modificational or exogenous diseases has been well expressed by one of the keenest workers in the Public Health service: "The nightmare of the specific inheritance of acquired diseases overloads the spontaneity of life, paralyses the will, and hampers the preventive service in its efforts to improve the environment. Weismannism exalts the social inheritances, which, as the great organs of selection, constitute the basis of preventive medicine" (W. Leslie Mackenzie).

(4) In regard to constitutional diseases, it seems on the whole that "the inheritance of predispositions to particular diseases" is a more accurate description of the facts that the common phrase, "the inheritance of disease." There is no doubt that many predispositions to particular constitutional diseases are inherited. What have we to set against this? We must recognise that every item in an inheritance requires an ap-

propriate nurture if it is to be expressed, or expressed fully, in development. This nurture is to some extent in our hands.

An organism with a predisposition to a constitutional disease —let us say albuminuria, asthma, gout, diabetes, or some nervous disorder—is obviously handicapped, more or less terribly according to the strength of the predisposition. There is a struggle for existence. But in this struggle a most momentous factor is nurture in the widest sense—the conditions of function and environment. If these favour the morbid elements in the inheritance, the organism has to fight a battle with two fronts, which is seldom hopeful. But if well-adapted conditions of life be secured, and secured early, there is always considerable hope that nurture may inhibit the full expression of the undesirable elements in the inherited nature.

(5) It seems to us that even expert writers have sometimes exaggerated the *necessity* of the persistence of constitutional taints and defects ; for as it is well known that a highly advantageous variation may fail to persist, why may not this be equally true of one that is highly disadvantageous ? A "retrograde variety"—that is, one which has lost one of the characteristics of the parent species—may arise in our garden and breed true. Why may not something analogous occur in a peculiarly vulnerable stock ? Why may not the vulnerability, the disadvantageous predisposition, disappear ? Apart from natural selection, sexual selection, and the like, it may be that the subtle process of germinal selection is sometimes able practically to eradicate an abnormal or morbid peculiarity.

(6) Crosses between wheat-plants immune to rust and others susceptible to rust yield hybrids which are all susceptible. But if these hybrids be inbred, the progeny are partly susceptible and partly immune, and all those that are immune breed true. If it is thus possible among plants "to get a pure thing out of an impure"—it may be that for domestic animals and for man himself the purification of a tainted stock is not a chimera.

(7) As to the diffusion of disease by the intermarriage of badly tainted with relatively healthy families, we have this in our own hands, and we need not whine over it. The basis of preferential mating is not unalterable; in fact, we know that it sways hither and thither from age to age. Possible marriages are every day prohibited or refrained from for the absurdest of reasons; there is no reason why they should not be prohibited or refrained from for the best of reasons—the welfare of our race.

By the education of conscience on a scientific basis there is already arising a wholesome prejudice against the marriage and especially the intermarriage of subjects in whom there is a strong hereditary bias to certain diseases—such as epilepsy and diabetes, to take two very different instances. Is it Utopian to hope that this will extend with increasing knowledge, and that the ethical consciousness of the average man will come more and more to include in its varied content "a feeling of responsibility for the healthfulness of succeeding generations"?

The argument always used against deliberate preferential mating on a eugenic basis is that our ignorance is immense. And this must be frankly admitted. Yet there are some things that we do know. We know that "the manifestly syphilitic subject who marries before he is thoroughly and definitely cured commits a crime, not only because there is the possibility—indeed, the probability—that he infects his wife, but also because he deliberately [*voraussichtlich*] begets syphilitic children. . . . The Eugenic office of the future, which will have to test applicants for a marriage-licence, not merely juristically or socially, but also biologically and medically, to decide as to their fitness for legitimate reproduction, will have no difficulty in refusing permission to uncured syphilitics and incurable drunkards, and perhaps also to those who are patently tubercular" (freely translated from Martius, 1905, p. 24).

That the best general constitutions should be mated is the first rule of good breeding.

That a markedly good constitution should not be paired with a markedly bad one is a second rule—a disregard of which means wanton wastage.

A third rule is that a person exhibiting a bias towards a specific disease should not marry another with the same bias. A man with a very marked phthisical tendency, if he marries at all, should not marry a woman whose family history is known to show many phthisical subjects.

In other words, every possible care should be taken of a relatively sound stock. The careless tainting of a good stock is a social crime. Every reasonable precaution should be taken to prevent a badly tainted stock from diffusing itself.

(8) Besides the advance of preventive medicine, the spreading enthusiasm for health, the awakening of a eugenic conscience, the suggestions as to "marriage-licences" and other forms of social selection, all making for the greater healthfulness of the human breed, we have, of course, to remember that our race has not got beyond the scope of natural selection, much as we try to evade it.

In the course of natural selection, keenest during the early years of life, the most tainted and the least immune or resistent tend continually to be "weeded out," and the standard of fitness is thus kept from falling rapidly. When predispositions to specific diseases accumulate (*e.g.* by in-breeding of similars), a non-viable, sometimes a non-reproductive, type arises, and—disappears for ever. Rotten twigs are always falling off the tree of life. There is a continual irrecoverable precipitation of incapables, who thus cease to muddy the stream.

But while this is true, every one is aware that man is so constituted that he cannot submit to Nature's winnowing. For reasons that go to the very foundations of our social frame-work, we can neither act as Spartan eliminators ourselves nor allow Nature to have her way. That this does not prevent us from being perhaps more cruel than either, is to be gravely feared, but

in any case, the fact is that we consistently try to conserve lives which natural selection would eliminate. This may be for social reasons necessary, but it cannot be regarded with satisfaction unless it is associated with positive selection of the fitter types.

It has often been said that modern hygiene, in tending to eliminate our eliminators—the microbes—is destroying a most valuable selective agency which has helped to make our race what it is.

It is difficult to find justification for the enthusiastic confidence which some seem to have in the value of microbes as eliminators. Which microbe? Surely not that of plague, which strikes indifferently, and is no more discriminatively selective than an earthquake. Surely not that of typhus, which used to kill weak and strong alike. Surely not that of typhoid, which may strike anyone, and does not confer more than a passing immunity. And so on through a long list.

It would perhaps be a subtler and more convincing line of argument to say that, throughout the ages, man has been selecting the microbes, lessening their virulence, in a sense taming them—sometimes to death—as his phagocytes were strengthened by more suitable food, or as his "Opsonic Index" improved, again perhaps in relation to food. As the body increases in its power of holding out—and this is demonstrably *modifiable*—it can prolong the contest with intruding microbes with more and more hope of ultimate victory.

In any case, whether microbes have been important and valuable selective agents or not, it is a sad confession on the part of the "paragon of animals" if he cannot discover other selective agencies—more discriminating, let us hope—to take the place of disease germs.

At present, we can only indicate that the future of our race depends on *Eugenics* (in some form or other), combined with the simultaneous evolution of *Eutechnics* and *Eutopias*. "Brave words," of course; but surely not "Utopian"!

CHAPTER IX

STATISTICAL STUDY OF INHERITANCE

"L'hybride est une mosaïque vivante."—NAUDIN.

The law of frequency of error "would have been personified by the Greeks, and deified if they had known of it."—FRANCIS GALTON.

§ 1. *Statistical and Physiological Inquiries.*
§ 2. *Historical Note.*
§ 3. *A Hint of the Statistical Mode of Procedure.*
§ 4. *Filial Regression.*
§ 5. *Law of Ancestral Inheritance.*
§ 6. *Criticisms of Galton's Law.*
§ 7. *Illustration of Results reached by Statistical Study.*

§ 1. *Statistical and Physiological Inquiries*

WHEN we study complex phenomena, such as the weather, we usually follow two methods. On the one hand, we may collect a multitude of observations—*e.g.*, as to the rainfall in different localities and at different times of year—and try from a careful scrutiny of these to make some general induction, which will show the inherent orderliness of sequences, even in such an apparently disorderly complex as the weather. On the other hand, we may give our attention to the actual mechanism of certain occurrences—*e.g.*, heavy rain with westerly winds and low barometric pressure—and seek to show how certain conditions are necessarily followed by certain results. In so doing, we fall back on the general laws of physics, and we may be

greatly assisted by crucial experiments—*e.g.*, on the *rôle* of atmospheric dust in connection with the precipitation of water vapour.

Similarly, in regard to the complex facts of inheritance we may pursue the same two methods. We may collect statistics as to the resemblances and differences—*e.g.* as regards stature, colour of eyes, intellectual ability, in successive generations—and try to arrive at some general induction, which will show the inherent orderliness even in a domain where occurrences seem at first sight as capricious as those of weather. On the other hand, we may focus our attention on the detailed course of events in particular cases—we may inquire, for instance, into the behaviour of the germ-cells before, during, and after fertilisation—and try to understand how certain conditions are necessarily followed by certain results. In so doing, we fall back on the general laws of biology, and we are greatly assisted by crucial experiments.

It is the aim of this chapter to *illustrate* what has been done by following the statistical method of inquiry into the facts of inheritance, and to state some of the inductions which have rewarded this mode of procedure. As the subject is not an easy one, and as it has been recently discussed by modern masters like Francis Galton and Karl Pearson, and in expository works such as Dr. H. M. Vernon's *Variation in Plants and Animals* (London, 1903), and Mr. R. H. Lock's *Variation, Heredity, and Evolution* (London, 1906), we shall confine ourselves to a brief sketch.

When we have to study results that depend upon numerous complicated conditions, the statistical method is of special service. Not that it can ever tell us how the conditions lead up to the results, but it will tell us what regularity there is in the occurrence of the results, and by displaying some unexpected correlation between certain antecedents and certain results, it may put us on the track of discovering the mechanism that

connects them. Thus, while every one knows that the stature attained by a thousand young men depends upon a multitude of dimensions of different parts of the body, and that these dimensions depend on numerous conditions, of which food is one, climate another, and parentage a third, we owe it to statistical methods that we are able to say definitely what relation the average height of these thousand sons bears to the average height of their fathers, that we are able to say, furthermore, that their stature depends more on the stature of their fathers than on that of their mothers. Thus we get a solid foundation for further inquiries of a deeper sort.

Again, to take another illustration, we know enough in regard to the results of four thousand throws of approximately symmetrical dice, to be able to say dogmatically, in regard to the quite divergent results of four thousand throws of other dice, that the latter must have been loaded. Similarly, as our knowledge of the laws of random sampling grows, we become able to detect when Nature's dice are loaded.

It should be clearly understood that the generalisation "Like begets like" may be much truer for the race at any given time than for any one relation of parents and offspring. Processes of selection in many forms tend to prune off peculiarities—operating even before birth, operating in very early stages of independent life, and never ceasing to operate—and thus one generation of a race may be very like the preceding generation, although in cases of *individual* heredity there may be marked differences between offspring and their parents. In short, it is very important to realise the distinction between individual heredity and race-heredity. The statistical study of inheritance enables us to do this.

§ 2. *Historical Note*

In order to appreciate the statistical point of view and the general ideas underlying its methods, the reader is advised to

read chapter xii. of J. T. Merz's invaluable *History of European Thought in the Nineteenth Century* (vol. ii., 1903, pp. 548–626). He traces the development of methods—*e.g.*: the investigations of Gauss and Laplace on the theory of error; he gives examples of their application—*e.g.* the kinetic theory of gases; and he shows how Quetelet was practically the first to apply statistical methods to human problems in his celebrated work *Sur l'Homme et le Développement de ses Facultés, ou Essai de Physique sociale* (1823).

But "the first who seems to have fully grasped the Darwinian problem from this (statistical) point of view is Mr. Francis Galton, who in a series of papers, and notably in his well-known works on *Hereditary Genius* (1869), and on *Natural Inheritance* (1889), made a beginning in the statistical treatment of the phenomena of Variation." "Mr. Galton's application of the theory of error to the facts of distribution and variation enabled him to bring method and order into such questions raised by the Darwinian theory as natural selection, regression, reversion to ancestral types, extinction of families, effect of bias in marriage, mixture of inheritance, latent elements, and generally to prepare the ground for the combined labours of the naturalist and the statistician" (Merz, p. 618).

Among those who have followed Mr. Galton's lead the most prominent and progressive worker is Prof. Karl Pearson, who has published numerous important mathematical contributions to the theory of evolution in the Transactions and Proceedings of the Royal Society since 1893, and in his journal *Biometrika*. The reader who is not prepared for much mathematics should consult the second edition of Pearson's *Grammar of Science*. See also his *Chances of Death and other Studies in Evolution* (2 vols., 1897).

§ 3. *A Hint of the Statistical Mode of Procedure*

Some idea of the mode of procedure in dealing statistically with the facts of inheritance may be got from the following

statement by an experienced statistician, Mr. G. Udny Yule (1902, p. 196):

"A series of measurements is made of some one variable character, *e.g.* a length, in parents and in their offspring, noting the individual families (the more the better) and not merely measuring the first generation as a whole and then their offspring as a whole. From these measurements an equation is derived, giving, as nearly as may be, the mean character of the offspring in terms of the character of the parent. Supposing X to be the character in the parent, Y the mean character in the offspring, then the simplest form of such equation is:

$$Y = A + B \cdot X,$$

where A is a dimension of the same order as X or Y, and B is a number that will vary from case to case. We have for instance, from the data collected by Mr. Galton for inheritance of stature in man, reduced by Prof. Pearson, the equation relating mean stature of sons and stature of father:

$$Y = 31{\cdot}10 + {\cdot}45\,X,$$

i.e. the mean stature of sons is 31·1 inches, together with nine-twentieths of the stature of the father (also in inches, of course). The father's stature is thus some guide to the stature of his offspring; it enables us to form a closer estimate of their stature than we could from a mere knowledge of the mean characters of the race, and we may therefore say that stature is an *inherited* character. The sons do diverge from the race-mean in the same direction as their parent. Quite generally, the statistician speaks of a character as *inherited* whenever the number or "constant" B is greater than zero; if it does not differ sensibly from zero the character is held to be non-heritable, quite apart from the question whether the mean is more or less constant from one generation to the next, a consideration which does not affect the conception of *individual* heredity."

§ 4. *Filial Regression*

It has often been remarked that the children of extraordinarily gifted parents are sometimes very ordinary individuals, and that the children of under-average parents sometimes turn out surprisingly well, both physically and mentally. Every one who has looked into the facts of inheritance in greater detail, and has compared the average of qualities in successive generations, has noticed in a general way that there is a tendency to sustain the same average level from generation to generation. Even the older inquirers, like Lucas, called attention to the fact that extraordinary qualities in families tend to wane away, as if there were some mysterious succession-tax levied on marked deviations from the average, whether in the way of excellence or of defect. But we owe to Mr. Francis Galton's careful statistical work the generalisation known as the Law of Filial Regression, which has replaced a vague impression by a definite formula. He has defined and measured that tendency towards mediocrity —that tendency to approximate to the mean or average of the stock, which is expressed by the term Filial Regression. We may notice at the outset that this has nothing to do with reversion or with degeneration, that it works upwards as well as downwards, forwards as well as backwards.

The data which Galton utilised were chiefly the *Records of Family Faculties*, obtained from about one hundred and fifty families, and dealing especially with stature, eye-colour, temper, artistic faculty, and some forms of disease. These were supplemented by measurements at Galton's anthropometric laboratory, and by observations on sweet peas and to some extent on moths.

Most trustworthy, however, were the data procured in regard to stature, which, as Galton points out, is a quality with many advantages as a subject of investigation. It is nearly constant during mature life, it is readily and frequently measured with accuracy, and it does not seem to be of appreciable moment in

sexual selection. Its variability, though small, is nearly normal; that is to say, the normal curve of the frequency of error nearly fits the distribution in many cases.

As the subject is by no means easy to those unaccustomed to statistical inquiry, and as we cannot within our limits explain the methods which Galton followed, it may be most profitable to give a few illustrative quotations from *Natural Inheritance* (1889).

"If the word 'peculiarity' be used to signify the difference between the amount of any faculty possessed by a man, and the average of that possessed by the population at large, then the law of Regression may be described as follows. Each peculiarity in a man is shared by his kinsmen, but *on the average* in a less degree. It is reduced to a definite fraction of its amount, quite independently of what its amount might be. The fraction differs in different orders of kinship, becoming smaller as they are more remote" (p. 194).

In the population with which Galton dealt the level of mediocrity in height was $68\frac{1}{4}$ inches (without shoes). The law or fact of regression which the statistics revealed was that the deviation of the sons from the mean of the population (P) is, on the average, equal to one-third of the deviation of the parent from P, and in the same direction. If $P \pm D =$ stature of the parent, then $P \pm \frac{1}{3}D =$ stature of the son. In these inquiries it is convenient to use the concept of a mid-parent, whose stature is half-way between the stature of the father and the "transmuted stature" of the mother, the last phrase meaning practically the stature that the mother would have if she were not female, *i.e.* an additional inch for every foot.

"However paradoxical it may appear at first sight, it is theoretically a necessary fact, and one that is clearly confirmed by observation, that the stature of the adult offspring must on the whole be more *mediocre* than the stature of their parents, that is to say, more near to the mean or mid of the general population" (p. 95).

While Galton's clearest results were obtained from data as to stature, the general conclusion was confirmed in regard to eye-colour, artistic faculty, and other qualities. There seems no reason to doubt the general occurrence of regression towards mediocrity, though it is doubtless modified in regard to characters which are subject to keen selection, either natural or sexual.

"The law of regression tells heavily against the full hereditary transmission of any gift. Only a few out of many children would be likely to differ from mediocrity so widely as their mid-parent, and still fewer would differ as widely as the more exceptional of the two parents. The more bountifully a parent is gifted by nature, the more rare will be his good fortune if he begets a son who is as richly endowed as himself, and still more so if he has a son who is endowed yet more largely. But the law is even-handed; it levies an equal succession-tax on the transmission of badness as of goodness. If it discourages the extravagant hopes of a gifted parent that his children will inherit all his powers, it no less discountenances extravagant fears that they will inherit all his weakness and disease" (p. 106).

"It must be clearly understood that there is nothing in these statements to invalidate the general doctrine that the children of a gifted pair are much more likely to be gifted than the children of a mediocre pair. They merely express the fact that the ablest of all the children of a few gifted pairs is not likely to be as gifted as the ablest of all the children of a very great many mediocre pairs" (p. 106).

Nor must the fact of regression be supposed to affect the general value of a good stock or the general disadvantage of a bad one. Two gifted members of a poor stock may be personally equivalent to two ordinary members of a good stock, but "the children of the former will tend to regress; those of the latter will not" (p. 198).

Let us give a concrete illustration from Prof. Karl Pearson's

Grammar of Science (1900, p. 454). "Fathers of a given height have not sons all of a given height, but an array of sons of a mean height different from that of the father and nearer to the mean height of sons in general. Thus take fathers of stature 72 inches, the mean height of their sons is 70″·8, or we have a *regression* towards the mean of the general population. On the other hand, fathers with a mean height of 66 inches give a group of sons of mean height 68″·3, or they have *progressed* towards the mean of the general population of sons. The father with a great excess of the character contributes sons with an excess, but a less excess of it; the father with a great defect of the character contributes sons with a defect, but less defect of it. The general result is a sensible stability of type and variation from generation to generation."

The quotations which we have given make the general idea of regression quite clear; for the detailed evidence and for further elaboration we must refer to the works of Galton and Pearson.

It is necessary, however, to ask what this statistically established fact of filial regression really means biologically.

Interpretation of Regression.—The facts of regression are expressed as a whole in the striking statistical resemblance between successive generations of a people. There is a continual tendency to sustain the specific average. It can hardly be denied that the similarity is in part the result of similar conditions, *e.g.*, of selection, but this hardly applies to the proportions persisting between tall and short, dark and fair, and so on. That it is not due to completeness of inheritance is obvious, for "the large do not always beget the large, nor the small the small"; the children do not in any precise way repeat the qualities of their parents. (Galton, 1889, pp. 1 and 116.) On what then does this regression depend?

Galton suggests two different reasons for the occurrence of regression (pp. 104, 105). The first is connected with his idea

of the stability of type, and may be thus expressed. This word "type" has for its central idea the existence of a limited number of recurrent forms—forms which have attained a considerable degree of organic stability. A deviation from the type may mean the attainment of a new position of organic equilibrium, and many "sports" are said to be very stable; but it may also mean a position of instability from which a regression to the old equilibrium is what might be expected. Just as certain kinds of cells have very definite dimensions, doubtless dependent in part on the optimum adjustment between the volume and the surface, so many animals have a very definite limit of growth, which doubtless represents a condition of constitutional equilibrium. Where this is the case, it is easy to understand that marked deviations in the direction of giants or in the direction of dwarfs would tend to be unstable. Their offspring may tend to regress to the position of stability simply because it is the physiological optimum in given conditions. The regulative phenomena in development would tend to secure the regression, in the same mysterious way as they secure the development of a perfect larva from a mutilated embryo. In the particular case of human stature, a deviation of a few inches may be quite immaterial, but it is easy to think of organisms in which the proportions of the various bodily dimensions are very important.

The other reason which Galton gives for the occurrence of regression is found in what may be called the fact of mosaic inheritance. The child inherits partly from its parents, partly from its ancestry. "In every population that intermarries freely, when the genealogy of any man is traced far backwards, his ancestry will be found to consist of such varied elements that they are indistinguishable from a sample taken at haphazard from the general population. The mid-stature M of the remote ancestry of such a man will become identical with P [the mean of the present population]; in other words, it will be mediocre."

"To put the same conclusion in another form, the most probable value of the deviation from P, of his mid-ancestors in any remote generation, is zero" (p. 105).

Pearson interprets Filial Regression in similar terms. "A man is not only the product of his father, but of all his past ancestry, and unless very careful selection has taken place the mean of that ancestry is probably not far from that of the general population. In the tenth generation a man has [theoretically] 1024 tenth great-grandparents. He is eventually the product of a population of this size, and their mean can hardly differ from that of the general population. It is the heavy weight of this mediocre ancestry which causes the son of an exceptional father to regress towards the general population mean; it is the balance of this sturdy commonplaceness which enables the son of a degenerate father to escape the whole burden of the parental ill. Among mankind we trust largely for our exceptional men to extreme variations occurring among the commonplace, but if we could remove the drag of the mediocre element in ancestry, were it only for a few generations, we should sensibly eliminate regression or create a stock of exceptional men. This is precisely what is done by the breeder in selecting and isolating a stock until it is established." (*Grammar of Science*, 1900, p. 456.)

Prediction.—When we know the heights of a thousand fathers of a given stock, and the heights of their sons, and the mean height of the general population, we have a basis for constructing a "regression equation," which may be used to calculate the *probable* stature of the son of any father. But this prediction may be wide of the mark, since exceptional individual variability often occurs. What will not be wide of the mark, however, is a prediction as to the average height of the sons of a group of, say, fifty fathers. If the formula [stature of son $= 38''{\cdot}45 + {\cdot}446 \times$ stature of father] be applied to fifty English middle-class fathers of the same height, it will be found that their sons have

an average height differing but little from that indicated by the formula. In regard to all these statistical conclusions, it must be carefully borne in mind that they cannot be applied to individual cases. "Of the individual we can assert nothing as certain, only state the probable. The individual varies owing to the variability of the gametes, and we know nothing of the particular gametes which fused to give the stirp, of which he is the product. All we know in heredity is what degree of resemblance there is on the average. . . . The statistician dealing with heredity is like the physicist dealing with the atom—he can say little or nothing of the individual, his knowledge is of the group containing great numbers." (Pearson, *op. cit.*, p. 457.)

Regression and Correlation.—As the term *regression*, used by Galton to describe the extent to which an average son is more like the mean of the stock than his father is, has been often misunderstood to imply something in the nature of a "throwback," it is probably desirable to get rid of it and to substitute for it the technical term *correlation*, which expresses the extent to which a son approximates nearer to his father than to the average of the stock.

The term "regression" which Mr. Galton introduced into biometry is not really a biological term. As the late Prof. Weldon pointed out in an interesting lecture, there may be regression between two different sets of results of dice-throwing if the second set of results is in some way, but not entirely, dependent upon the first. He protested against regarding regression "as a peculiar property of living things, by virtue of which variations are diminished in intensity during their transmission from parent to child, and the species is kept true to its type" (1906, p. 107).

If a set of fathers deviate, in respect to some character, a certain amount from the general mode of the whole population, their sons will, in respect to the same character, vary about a mode which is between the paternal deviation and the mode of the whole population. This is filial regression.

Now, the amount of the regression affords a useful measure of the intensity of the inheritance. If the regression is slight, it means that the intensity of the inheritance is high; if the regression is considerable, it means that the intensity of the inheritance is low. The ratio between the deviation of sons in general and the deviation of their fathers in general in respect to a given character gives a measure of the intensity of inheritance for that character, and is called the "coefficient of correlation." A simple and very clear account of the way of obtaining a "coefficient of correlation" will be found in Doncaster's *Heredity*, 1910, chap. iv.

The correlations worked out by Pearson and others for a number of characters in plants, animals, and man, vary between 0·42 and 0·52, which means that on the average the offspring deviate from the mean of the general population about half as much as the parent.

"It seems likely that in cases where the mating of parents is not determined to any serious extent by their likeness or unlikeness in the character discussed, the regression of children on parents has a value very nearly the same, and very nearly equal to $\frac{1}{2}$, for a large series of characters, mental as well as physical, in human beings, and for a large series of characters in the higher animals, at all events, if not in animals generally" (Weldon, 1906, p. 108).

Summary.—Many individual organisms differ markedly from the mean of the stock or race to which they belong. In some character or characters they are extraordinary individuals. What is the chief conclusion in regard to the offspring of these individuals? It is that *they are, on an average, more mediocre than their parents.*

As Mr. Yule puts it, "This phenomenon of the relapse of the offspring from the parental type towards mediocrity is termed *regression.* Regression and not constancy of type is, for the statistician, the fundamental phenomenon of heredity and the

prime fact to be explained by any physical theory" (1902, p. 197).

It is explained on the general assumption that an inheritance is a mosaic made up of contributions from a complex of ancestors which when traced say to a tenth generation back correspond to an average sample of the stock in question.

Note on Reduction of Ancestors.—To appreciate the possible complexity of our mosaic inheritance we must recall the number of our ancestors. We have two parents, four grandparents, eight great-grandparents, about sixteen great-great-grandparents, and so on. "If," as Prof. Milnes Marshall said, "we allow three generations to a century, there will have been twenty-five since the Norman Invasion, and a man may be descended not merely from one ancestor who came over in 1066, but directly and equally from over sixteen million ancestors who lived at or about that date." But on these theoretical lines the existence of one man to-day would involve the existence of nearly seventy thousand millions of millions of ancestors at the commencement of the Christian era. Which is absurd. What the theoretical scheme fails to take account of is the frequent occurrence of close intermarriage—of cousins for instance. When we are dealing with a large group of families, we find individual ancestors figuring in different genealogical trees.

Brooks (*Science*, 1895, p. 121) points out that if the population of a given district had for ten generations married first cousins the total ancestry of each person would be only thirty-eight, instead of the theoretical possible 2046. "An investigation into the ancestry of three persons, not nearly related, living on an island on the Atlantic coast where the records are complete for seven and eight generations, shows that the ancestry of each of the three averages only 382 persons" (Cope, 1896, p. 460).

The problem of reduction in the number of ancestors has been very carefully discussed by genealogists like Prof. Lorenz and Dr. F. T. Richter. We must be content to take one example. Theoretically, Kaiser Wilhelm II. might have had in the direct line the number of ancestors indicated in the upper row on the next page; the second row indicates the number actually known, on to the twelfth generation; the third row gives the number of those

possible ancestors of whose existence there is deficient record; and the fourth row gives the probable total.

Generations	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
(1) Theoretical number	2	4	8	16	32	64	128	256	512	1024	2048	4096
(2) Actual number known.	2	4	8	14	24	44	74	111	162	200	225	275
(3) Inadequately known.								5	15	56	117	258
(4) Probable total.								116	177	256	342	533

§ 5. *Law of Ancestral Inheritance*

In all ordinary cases of reproduction the offspring has a strictly dual or bi-parental inheritance. Whether the inheritance be blended, particulate, or exclusive in its expression, it is made up, to begin with, of equal contributions from the two parents. Obviously, however, if the concept of the continuity of the germ-plasm be correct, the contribution from the father is made up of contributions from his two parents, and the contribution from the mother is made up of contributions from her two parents. And so on backwards. Thus we reach the idea, so often referred to in this volume, that an individual inheritance is a mosaic of ancestral contributions. Incidental corroborations of this fruitful idea are familiar to all—*e.g.* in the re-expression of trivial details which were characteristic features of, say, the grandfather or the great-grandmother. To Mr. Galton's careful statistical work, however, we owe a generalisation which formulates the share which the various ancestors have on an average in the inheritance of any individual organism. This is the Law of Ancestral Inheritance.

Galton's Statement of his Law.—Mr. Galton based his generalisation on data as to stature and other qualities in man and as to coat-colour in Basset hounds. His law is as follows: "The two parents between them contribute *on the average* one-half of each inherited faculty, each of them contributing one-quarter of it. The four grandparents contribute between them

one-quarter, or each of them one-sixteenth; and so on, the sum of the series $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \ldots$, being equal to 1, as it should be. It is a property of this infinite series that each term is equal to the sum of all those that follow: thus $\frac{1}{2} = \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \ldots$, $\frac{1}{4} = \frac{1}{8} + \frac{1}{16} + \ldots$, and so on. The prepotencies or sub-potencies of particular ancestors, in any given pedigree, are eliminated by a law that deals only with *average* contributions, and the varying prepotencies of sex in respect to different qualities are also presumably eliminated." Thus an inheritance is not merely dual, but through the parents it is multiple, and the *average* contributions made by grandparents, great-grandparents, etc., are definite, and diminish in a precise ratio according to the remoteness of the ancestors.

The idea of diminution according to remoteness of ancestry may be made more concrete by looking at some of the tables in Galton's *Hereditary Genius* (1869). Thus 100 eminent men have about 31 eminent fathers, 17 eminent grandfathers, and 3 eminent great-grandfathers.

Diagrammatic Expression.—The proportions contributed on an average by the parents, grandparents, great-grandparents, etc., may be seen at a glance from a diagram (on the opposite page) which we have borrowed from one of Mr. Galton's papers.

Pearson's Statement of Galton's Law.—Prof. Karl Pearson states Galton's law in the following form: "Each parent contributes on an average one-quarter or $(0{\cdot}5)^2$, each grandparent one-sixteenth or $(0{\cdot}5)^4$, and so on; the occupier of each ancestral place in the *n*th degree, whatever be the value of *n*, contributes $(0{\cdot}5)^{2n}$ of the heritage." He calls attention to the extreme importance of the law, for "if Darwinism be the true view of evolution—*i.e.* if we are to describe evolution by natural selection combined with heredity—then the law which gives us definitely and concisely the type of the offspring in terms of the ancestral peculiarities is at once the foundation-stone of biology and the basis upon which heredity becomes an exact branch of science"

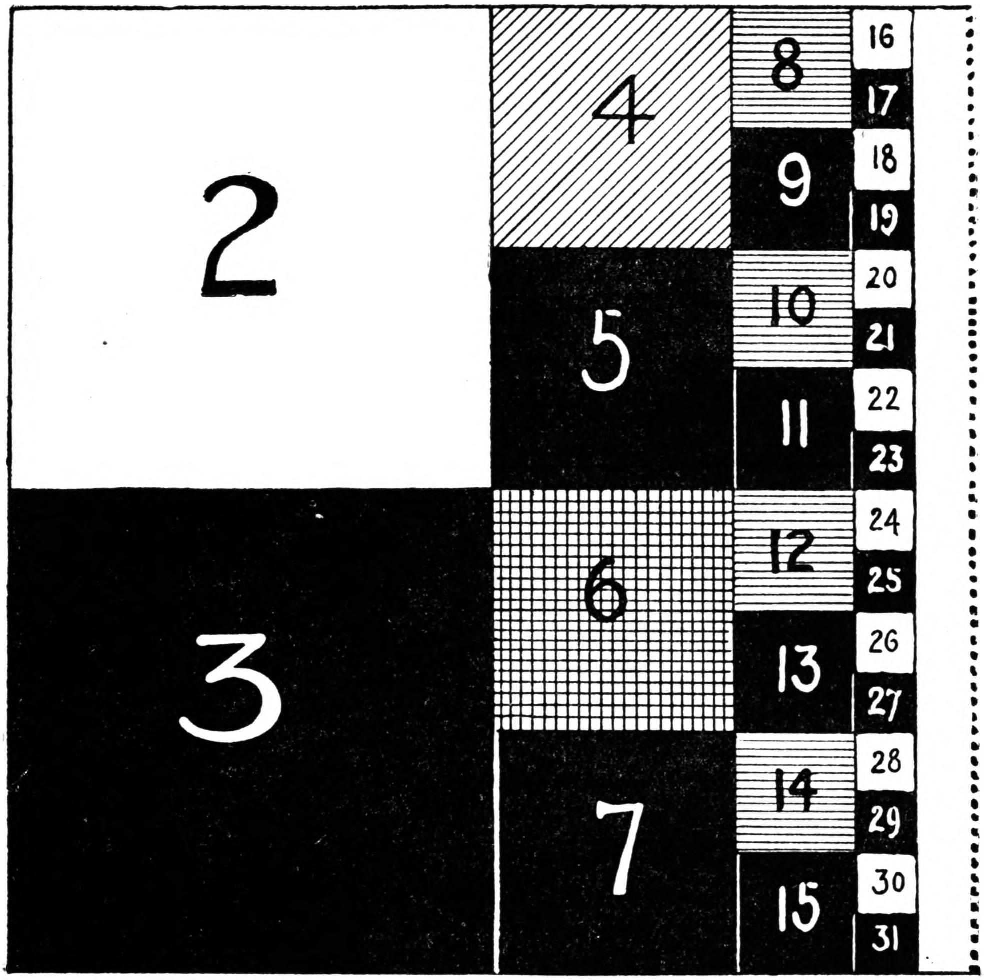


FIG. 29.—Diagram illustrating Galton's Law of Ancestral Inheritance. (After Galton.) The figure was originally due to Mr. A. J. Meston (*The Horseman*, Chicago, Dec. 28, 1897).

"The area of the square diagram represents the total heritage of any particular form or faculty that is bequeathed to any particular individual. It is divided into subsidiary squares, each bearing distinctive numbers, which severally refer to different ancestors. The size of these subsidiary squares shows the average proportion of the total heritage derived from the corresponding ancestors. . . . The subject of the pedigree may be called 1. Thenceforward whatever be the distinctive number of an ancestor, which we will call n, the number of its sire is $2n$, and that of its dam is $2n+1$. All male numbers in the pedigree are therefore even and all female numbers are odd. To take an example—2 is the sire of 1, and 3 is the dam of 1; 6 is the sire of 3 and 7 is the dam of 3. Or, working backwards, 14 is a male who is mated to 15; their offspring is 7, a female, who is mated to 6; their offspring is 3, a female, who is mated to 2, and their offspring is 1, the subject. . . . The numbered squares could be continued indefinitely; in this small diagram they cease with the fourth generation, which contributes a 16th part of the total heritage, therefore the whole of the more distant ancestry, comprised in the blank column, contributes one-sixteenth also" (Galton, 1898).

(*Grammar of Science*, 1900, p. 479). Elsewhere he says: "The law of ancestral heredity is likely to prove one of the most brilliant of Mr. Galton's discoveries; it is highly probable that it is the simple descriptive statement which brings into a single focus all the complex lines of hereditary influence. If Darwinian evolution be natural selection combined with heredity, then the single statement which embraces the whole field of heredity must prove almost as epoch-making to the biologist as the law of gravitation to the astronomer."

Prof. Karl Pearson has himself given a statement of the law of ancestral inheritance somewhat different from Galton's, but his methods and general results are practically the same. The following quotation (1903a, p. 215) is useful:

"Taking our stand, then, on the observed fact that a knowledge neither of parents nor of the whole ancestry will enable us to predict with certainty in a variety of important cases the character of the individual offspring, we ask: What is the correct method of dealing with the problem of heredity in such cases? The causes A, B, C, D, E, . . . which we have as yet succeeded in isolating and defining are not always followed by the effect X, but by any one of the effects U, V, W, X, Y. We are, therefore, not dealing with causation but correlation, and there is, therefore, only one method of procedure possible; we must collect statistics of the frequency with which U, V, W, X, Y, Z, respectively follow on A, B, C, D, E. . . . From these statistics we know the most *probable* result of the causes A, B, C, D, E, and the frequency of each deviation from this most probable result. The recognition that in the existing state of our knowledge the true method of approaching the problem of heredity is from the statistical side, and that the most that we can hope at present to do is to give the *probable* character of the offspring of a given ancestry, is one of the great services of Francis Galton to biometry."

Pearson has worked out the average correlation between off-

spring and their parents, their grandparents, and so on backwards. He finds that the correlation between offspring and parent is about 0·5, between offspring and grandparent 0·33, between offspring and great-grandparent 0·22. These figures indicate the degree of resemblance, in respect of a character measured, between offspring and an ancestor of each generation. From these he has worked out the average ancestral contributions, and he has been led to conclude that the series 0·6244, 0·1988, 0·0630, etc., is more accurate than Galton's series 0·5, 0·25, 0·125, etc.

Summary.—Galton formulated his Law of Ancestral Inheritance as follows: "The two parents contribute between them on the average one-half or (0·5) of the total heritage of the offspring; the four grandparents, one-quarter, or $(0{\cdot}5)^2$; the eight great-grandparents, one-eighth, or $(0{\cdot}5)^3$, and so on. Thus the sum of the ancestral contributions is expressed by the series $[(0{\cdot}5) + (0{\cdot}5)^2 + (0{\cdot}5)^3$, etc.], which, being equal to 1, accounts for the whole heritage" (1897, p. 402).

But it is quite legitimate to accept the general idea of this Law without accepting the fixity of the fractions of partial inheritance which it expresses.

Mr. G. Udny Yule states the law of ancestral heredity in the most general way possible when he says: "This law, that *the mean character of the offspring can be calculated with the more exactness, the more extensive our knowledge of the corresponding characters of the ancestry*, may be termed the Law of Ancestral Heredity" (1902, p. 202).

Prof. Weldon (1902) states the law of ancestral inheritance in the following terms: "*The degree to which a parental character affects offspring depends not only upon its development in the individual parent, but on its degree of development in the ancestors of that parent.*" Mr. Yule suggests that, instead of the word "affects," which to some extent implies a direct physical influence, it would be more accurate to read "serves as a basis for estimating the character of."

In a later paper Prof. Weldon discussed the validity of Galton's Law, and wrote as follows:—

". . . The results so far achieved make it probable that Mr. Galton's original prediction will be verified for the large class of cases to which he intended it to apply, and that the influence of the different generations of ancestors, as measured by the regression coefficients between these and existing individuals, will be found to diminish with the remoteness of the ancestors, according to the terms of a simple geometric series, which is sensibly the same at least for all those characters among the higher animals which have been properly examined" (Weldon, 1906, p. 108).

§ 6. *Criticisms of Galton's Law*

Since the importance of the law is great, we must devote some attention to certain criticisms which have been made. It goes without saying that those who wish to criticise the basis on which the generalisation is founded must consult the original documents, referred to in the bibliography.

It must be borne in mind that the Law of Ancestral Inheritance is a statistical conclusion dealing with what is true on an average for a large number of cases. To say that we know of particular cases where it does not hold—where, for instance, the amount of resemblance between an individual and his paternal grandfather is far greater than is represented by the theoretical fraction—is no argument against the induction. It is like saying that the statistics showing the percentage of deaths in cases of scarlet fever must be wrong because we know of large families which were visited by the disease without a single fatal result!

It may be urged against the crispness of Galton's Law, (1) that the hereditary relation is a complex affair; (2) that most organic qualities, and the amounts of resemblance in successive

generations, can seldom be measured with the accuracy possible in the case of a quality like stature; and (3) that the actual quota of any character which forms part of a heritage is something different from the expression which that quota finds in development—for the expression depends in part on the conditions of nurture. For these and similar reasons it may seem suspicious that the fractions indicating the average contributions of parents, grandparents, great-grandparents, etc., should be representable in such a simple series as $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \ldots$

The general answer is, of course, that when the data are large enough, the irregularities of result due to particular peculiarities, such as a highly prepotent great-grandfather, are smoothed out.

While Galton sometimes spoke of his law in its physiological aspect, there can be no doubt that he regarded it in the main as a statistical description, dealing with average inheritances, and applying to masses rather than to the component individuals considered separately. Thus he distinctly says (1897, p. 402): "The neglect of individual prepotencies is justified in a law that avowedly relates to average results."

Darbishire has tried by means of a diagram to clear up the prevalent confusion which opposes statistical and physiological formulæ. In the figure there is a diagrammatic representation of four successive generations; a^1, b^1, x^1; a^2, b^2, x^2, etc. represent adult individuals of these generations; α^1, β^1, $\omega^{1\prime}$; α^2, β^2, ω^2, etc., represent the germ-cells produced by those individuals. Now the statistical formulation contents itself with keeping above the line A—B, and deals with the successive generations as generations, stating the relation of hereditary resemblance which subsists between them. But the physiological interpretation seeks to penetrate below the line A—B, and seeks to show by a theory of germinal contributions how it is that α^1 gives rise to α^2, which may be more or less

different, how a^2 gives rise to a^3, which again may be more or less different.

To bring out the contrast between statistical and physiological conclusions, Darbishire refers to the familiar riddle, "*Why do white sheep eat more than black ones?*" with its answer "*Because there are more of them.*" "When you ask the riddle you do not say that you are not referring to individual white and black sheep, but the man of whom the riddle is asked *invariably* thinks you are"—with interesting consequences. "If he is a biologist he may be trying to think of some physiological explanation of the fact,

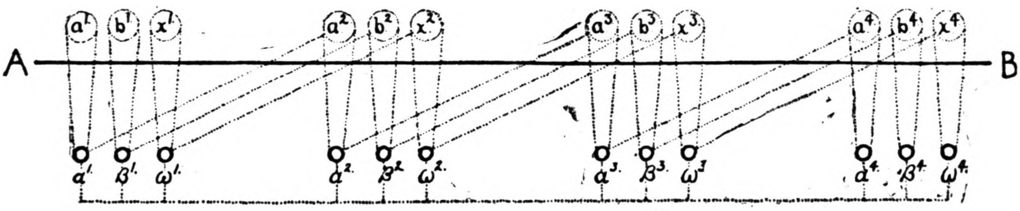


FIG. 30.—Diagram to illustrate the difference between statistical and physiological formulation. (After Darbishire.)

in connection possibly with the well-established relation between pigmentation and the getting rid of waste products." "In the answer he is told that the amount eaten by the sum-total of white sheep as compared with that eaten by the sum-total of black sheep is the subject under discussion."

"If the antithesis between truths about masses, and truths about individuals, which constitutes the point in this riddle, were more widely and more clearly perceived than it is to-day, there would no longer be that confusion in the minds of most biologists which prevents them seeing the profound difference that exists between a physiological law like Mendel's, which is true of units, and a statistical one like the Law of Ancestral Inheritance, which is true of masses. All intending students of heredity should be asked this riddle; and if they cannot detect the fallacy in it they should be declared unfit for their intended task."

Some Saving Clauses.—(*a*) The laws of ancestral inheritance and of filial regression are average statements as regards the

distribution of hereditary qualities, not physiological generalisations in regard to individuals. There is no mysterious force of filial regression, causing offspring to gravitate towards mediocrity. There is a statistically observed tendency to keep up an average in a stock, and the explanation offered of the fact is that each offspring has a multiple ancestry, and that this soon resolves itself into a mediocre sample of the general population. It may be, however, that there is a fallacy in the theory, namely in the assumption that the degree of resemblance observed is wholly due to heredity. Much resemblance may be due to similarity in nurture, to non-transmissible somatic modifications which are re-impressed generation after generation by peculiarities of environment, nutrition, and function. Pearl (1915) and others have pointed out that heredity is not the sole cause which can lead statistically to a significant correlation between parent and offspring. Conklin (1918, p. 221) writes: "The value of statistics depends upon a proper classification of the things measured and enumerated, and if things which are not commensurable are grouped together the results may be quite misleading and worthless. Unfortunately Galton and Pearson, as well as some of their followers, have not carefully distinguished between hereditary and environmental characters." Jennings (1910) says: "Galton's laws of regression and ancestral inheritance are the product mainly of a lack of distinction between two absolutely diverse things, between non-inheritable fluctuations on the one hand" (our "somatic modifications") "and permanent genotypic differentiations" (our "germinal variations and mutations") "on the other."

(*b*) Galton and Pearson pointed out that the generalisations in question do not hold in lineages where very careful selection has taken place, for in such cases the mean of the ancestry was obviously different from that of the general population.

(*c*) The law of ancestral inheritance was a statistical conclusion intended to show the proportionate average contribution

that each ancestor makes to the individual's inheritance. But it does not seem to be applicable in regard to non-blending Mendelising characters. It is premature to abandon belief in the reality of blending hereditary characters to which the Galtonian statistical formulations may apply.

§ 7. *Illustration of Results reached by Statistical Study*

While we can neither explain the methods nor summarise the arguments, it may be permissible to cite some of the results reached by the statistical study of inheritance, always bearing in mind the caution that the validity of a statistical result, like the validity of any other scientific result, depends on the value of the data. The world of organisms is very large and heterogeneous, and results that hold good for certain forms of life may not be true of others.

It has been shown statistically that in the human race the father is prepotent in the matter of stature, and this for offspring of both sexes (Pearson).

It has been shown statistically that a subtle quality like fertility is a heritable quality, and more detailed statements can be made—*e.g.* that the woman inherits fertility equally through the male and female lines.

The immediate practical bearing of some of these researches is evident. Thus Messrs. Rommel and Philipps (1906) have shown in regard to Poland China hogs: (1) that there has been an increase of ·48 in the size of litter in the twenty years between 1882 and 1902, and (2) that the size of litter is a character transmitted from mother to daughter. "It would appear proved that, by judicious selection for breeding purposes of sows from large litters, the average for the breed may be increased."

Prof. Karl Pearson has been led by rigorous statistical methods to statements like the following:—

"If selection were to act upon our 5′ 9″ Englishmen, and the 6′ among them were the type best fitted to survive, then with fairly stringent selection it would not take more than six generations to produce a type sensibly 6′ high, and this type would be permanently established even if selection ceased. . . . Our determination of the quantitative strength of heredity is thus seen to give values quite intense enough to produce

rapid and permanent changes of type, when selection is stringent."

Prof. Pearson has worked out the following case. Suppose the mean height of a population be 5′ 8″, that a start is made with individuals 6′ 2″, and that for successive generations individuals of this height are selected as parents. It is calculated that in the first generation the offspring would show 0·62 of the particular quality selected (h), viz. 6″ of deviation above the general mean height. It is calculated that after two generations the offspring will show 0·82h, after three generations 0·89h, and so on up to 0·92h. Thus by persistent selection an array of individuals would result, almost all of whom were over six feet in height.

But if at a given generation the artificial selection of tall parents stops, and the tall array is left to inbreed, there will be a gradual sinking back towards the mean height of the population.

The importance of definite conclusions of this kind can hardly be overestimated.

"Looked at from the social standpoint, we see how exceptional families, by careful marriages, can within even a few generations obtain an exceptional stock, and how directly this suggests assortative mating as a moral duty for the highly endowed. On the other hand, the exceptionally degenerate isolated in the slums of our modern cities can easily produce permanent stock also: a stock which no change of environment will permanently elevate, and which nothing but mixture with better blood will improve. But this is an improvement of the bad by a social waste of the better. We do not want to eliminate bad stock by watering it with good, but by placing it under conditions where it is relatively or absolutely infertile" (Pearson, *Grammar of Science*, p. 486).

By statistical methods Pearson has reached the interesting conclusion that while blended inheritance illustrates *regression*, it is to cases of exclusive inheritance that we should look for

reversion (*i.e.* the reappearance of a character which occurred in a definite ancestor). In exclusive inheritance, in which the offspring inherits the full character of either parent, and does not blend the two, the law of ancestral inheritance in the strict sense ceases to hold, for it presupposes a blend. Thus eye-colour in man rarely, if ever, blends, and it is in regard to such characters that we should look for reversion.

By statistical methods Pearson has sought to ascertain how far the inheritance of *the duration of life* extends, and has reached the important conclusion that in a large percentage of cases there is evidence in the death-rate that discriminate selection is at work. It is no longer possible to say of natural selection, as Lord Salisbury did in 1894, that "no man, so far as we know, has seen it at work." "It is at work, and at work among civilised men, where intra-group struggle—*i.e.*, autogeneric selection—is largely suspended, with an intensity of a most substantial kind. Of the existence of natural selection there can be no doubt; we require careful experiments and observation to indicate the rapidity of its action. In a few years we may hope no longer to hear natural selection spoken of as hypothetical, but rather to listen to a statement of its quantitative measure for various organisms under divers environments" (*Grammar of Science*, p. 500).

CHAPTER X

EXPERIMENTAL STUDY OF INHERITANCE

As regards Mendel's Law, "The experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the atomic laws of chemistry."—BATESON.

"The breeding-pen is to us what the test-tube is to the chemist—an instrument whereby we examine the nature of our organisms and determine empirically their genetic properties."—BATESON.

"That Hurst can predict the difference between the result of mating two pairs of rabbits externally identical, by means of a knowledge of the difference between their gametic constitutions acquired by previous breeding from them, constitutes, it seems to us, the longest stride the study of heredity has made for some time past."—*Nature*, lxxi. 1905, p. 315.

§ 1. *Mendel's Discoveries.*
§ 2. *Theoretical Interpretation.*
§ 3. *Corroborations.*
§ 4. *Illustrations of Mendelian Inheritance.*
§ 5. *Mendel's Discovery in Relation to Other Conclusions.*
§ 6. *Practical Importance of Mendel's Discovery.*
§ 7. *Other Experiments on Heredity.*
§ 8. *Consanguinity.*

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§ 1. *Mendel's Discoveries*

IN 1866 Gregor Johann Mendel,* Abbot of Brünn, published what some regard as one of the greatest of biological discoveries. After many years of patient experimenting, chiefly with the

* Gregor Johann Mendel was born in 1822, the son of well-to-do peasants in Austrian Silesia. He became a priest in 1847, and studied physics

edible pea, he reached a very important conclusion in regard to the inbreeding of hybrids, which is often briefly referred to as "Mendel's Law." His publication was practically buried in the *Proceedings of the Natural History Society of Brünn;* those who knew of it, as Nägeli for instance did, failed to realise its importance: in fact, Mendel's epoch-making work was lost sight of amid the enthusiasm and controversy which the promulgation of Darwinism (1858) had evoked. Mendel's Law seems to have been rediscovered independently in 1900 by the botanists De Vries, Correns, and Tschermak; and to Mr. Bateson we owe much, not only for his recognition of the far-reaching importance of the abbot's work, but also for a notable series of experiments in which he has confirmed and extended it.

Mendel's Experiments.—What Mendel sought to discover was the law of inheritance in hybrid varieties, and he selected for experiment the edible pea (*Pisum sativum*). The trial plants, he says, must possess constant differentiating characters, and must admit of easy artificial pollination; the hybrids of the plants must be readily fertile, and readily protectable from the influence of foreign pollen. These conditions were afforded by peas, and twenty-two varieties or subspecies of pea were selected, which remained constant during the eight years of the experiments. Whether they are called species, or subspecies, or varieties, is a matter of convenience; the names *Pisum quadratum, P. saccharatum, P. umbellatum,* etc., do in any case represent groups of similar individuals which breed true *inter se.* It

and natural science at Vienna from 1851 to 1853. Thence he returned to his cloister and became a teacher in the Realschule at Brünn. It was his hobby to make hybridisation experiments with peas and other plants in the garden of the monastery, of which he eventually became abbot. Apart from two papers, one dealing with peas and a shorter one with hawkweeds, and some meteorological observations, he does not seem to have published much. But what he did publish, if small in quantity, was large in quality. He died in 1884.

should be noted that these peas have the particular advantage, for experimental purposes, that they are habitually self-fertilised —in North Europe, at least.

In studying the different forms of peas, Mendel found that there were seven differentiating characters which could be relied on:

1. The form of the ripe seeds, whether roundish, with shallow wrinkles or none, or angular and deeply wrinkled;
2. The colour of the reserve material in the cotyledons—pale yellow, bright yellow, orange, or green;
3. The colour of the seed-coats, whether white, as in most peas with white flowers, or grey, grey-brown, leather brown, with or without violet spots, and so on;
4. The form of the ripe pods, whether simply inflated, or constricted, or wrinkled;
5. The colour of the unripe pods, whether light or dark green, or vividly yellow, this colour being correlated with that of stalk, leaf-veins, and blossoms;
6. The position of the flowers, whether axial or terminal; and
7. The length of the stem, whether tall or dwarfish.

Mendel's Results: The Law of Dominance.—Having defined the differentiating characteristics of the varieties, Mendel proceeded to make crosses between these, investigating one character at a time. Thus, pollen from a pea of the round-seeded variety was transferred to the stigma of a pea of the angular-seeded variety, the stamens of the artificially pollinated flower being, of course, removed before they were ripe. The same was done all along the line.

What was the result in the hybrid or cross-bred offspring? It was found that they showed *one* of each pair of contrasted characters, to the total, or almost total, exclusion of the other. No intermediate forms appeared.

Mendel called the character that prevailed *dominant*, and the character that was suppressed, or apparently suppressed, *recessive*. And the first big result was that crosses between a plant with the dominant character and a plant with the recessive

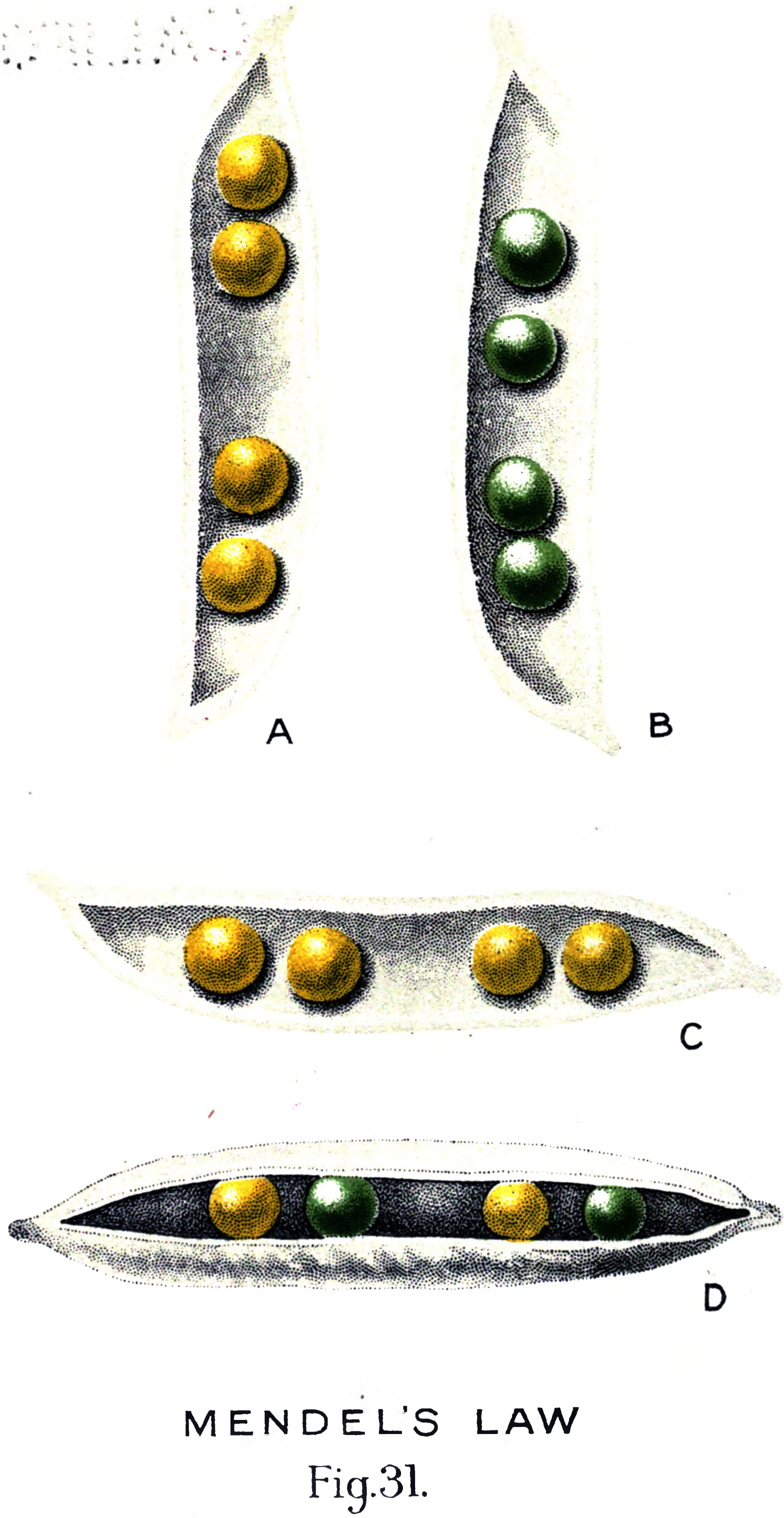

FIG. 31.—Peas showing Mendel's Law.

A, Pod of yellow-seeded (dominant) parent; B, Pod of green-seeded (recessive) parent; C, Pod of hybrid offspring—all with yellow seeds (F^1); D, Pod showing the splitting up of the next self-fertilised generation (F^2) into yellow-seeded and green-seeded.

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character yielded offspring all resembling the dominant parent as regards the character in question. Let us for shortness call the parents D and R, and the first result may be expressed thus: $D \times R = D$.

It must be carefully noted that the *complete* dominance which Mendel observed has been shown in other cases to be the exception rather than the rule. Thus a cross between a "Chinese" primula with wavy crenated petals and a "star" primula with flat simply notched petals is intermediate between the two parents; and yet, as the next generation shows, the case is one of Mendelian inheritance.

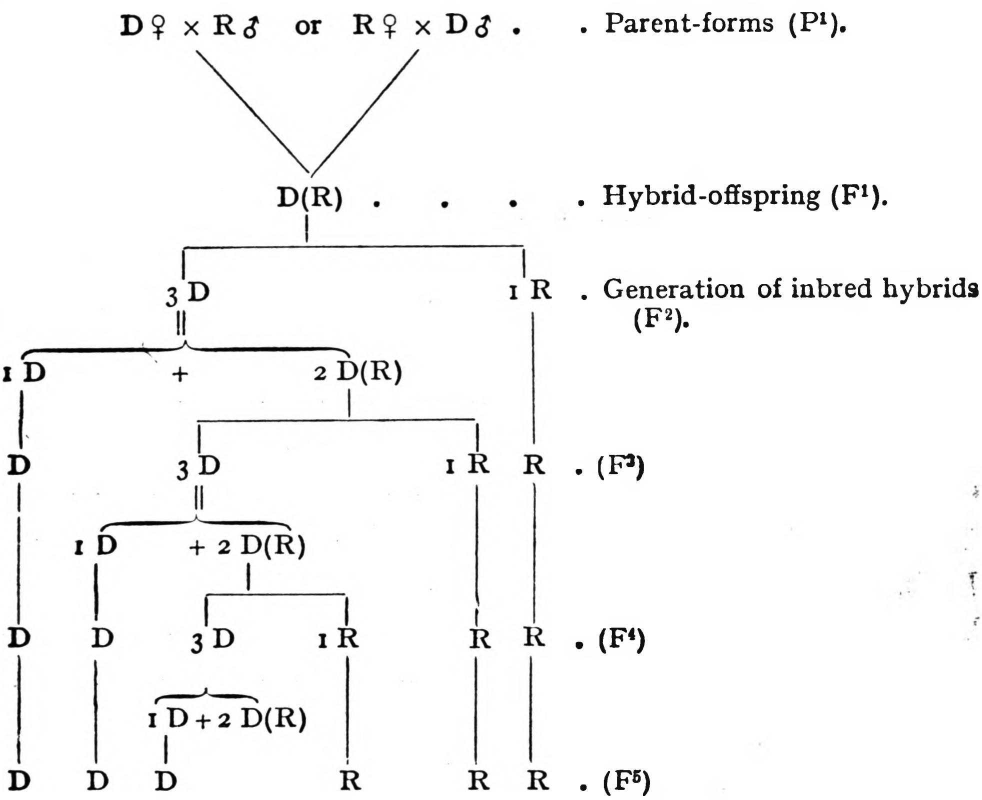
In many cases the hybrid, while on the whole dominant, may show some influence of the recessive character, but not nearly enough to warrant us in speaking of a blend. Thus, when white (dominant) Leghorn poultry are crossed with brown (recessive) Leghorn, most of the offspring have some "ticks" of colour. When these are inbred they produce a quarter brown (extracted recessives) and three-quarters pure white or white with a few ticks. The dominance is not quite perfect.

The Law of Splitting or Segregation.—In the next generation the cross-bred plants (products of D and R, or R and D, but all apparently like D) were allowed to fertilise themselves, with the result that their offspring exhibited *the two original forms*, on the average three dominants to one recessive. Out of 1,064 plants, 787 were tall, 277 were dwarfs.

When these recessive dwarfs were allowed to fertilise themselves they gave rise to recessives only, for any number of generations. The recessive character bred true.

When the dominants, on the other hand, were allowed to fertilise themselves, one-third of them produced "pure" dominants, which in subsequent generations gave rise to dominants only; and two-thirds of them produced once again the characteristic mixture of dominants and recessives in the proportion of 3 : 1.

The general results may be expressed in the following scheme :—



The result of the hybridisation is a generation (F1) like the dominant parent. They may be represented by the symbol D(R), for they carry with them the possibility of having offspring with the recessive character; that is to say, the recessive character remains latent in the inheritance.

When these D(R)s are inbred (self-fertilised, in the case of peas) they have offspring (F2), some of which resemble the recessive parent, while others resemble the dominant parent, and these occur in the proportion of 1 : 3. When those resembling the recessive parent are inbred, they breed true—*i.e.* they give rise to a line of pure recessives. Those resembling the dominant parent are all apparently alike, but their subsequent history shows that they may be divided into a set which breed true to the

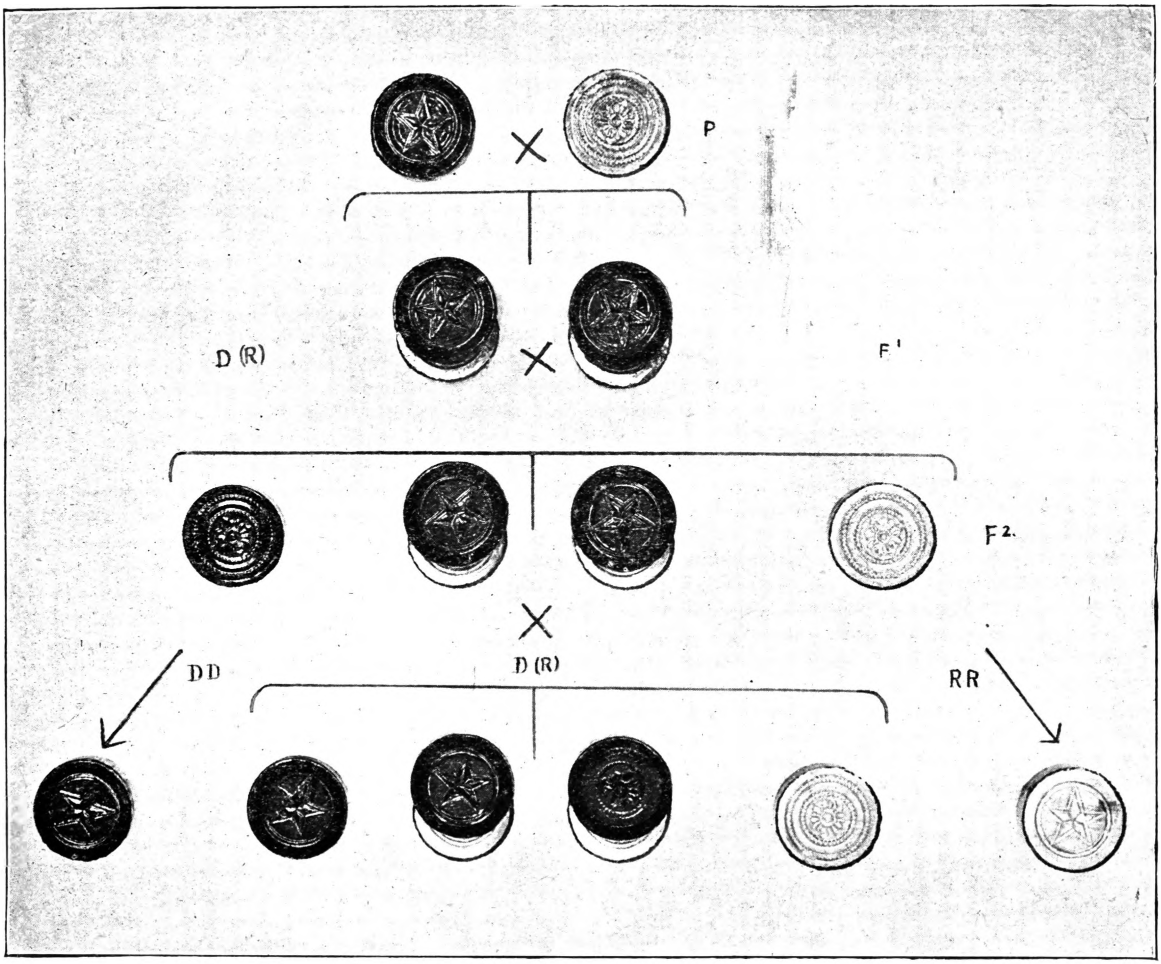


FIG. 32.—Diagram, photographed from draughtsmen, to illustrate Mendel's Law.

First line (P) a black dominant and a white recessive. Second line (F^1) the hybrid offspring D(R), the black patent, the white latent below. Third line (F^2) one "pure" black, two "impure" blacks, and one "pure" white, 1DD+2D(R)+1RR. Fourth line pure extracted dominant to the extreme left, pure extracted recessive to the extreme right; in the middle, as usual, 1DD+2D(R)+1RR.

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dominant type and a set which behave like the first generation of hybrids—*i.e.* they go on splitting up into dominant-like forms and pure recessives. These two sets occur in the proportions of 1 : 2.

A Case of Peas.—Let us consider a concrete case. Peas with rounded seeds were crossed with peas having angular wrinkled seeds. In the offspring the character of roundness was dominant; the angular wrinkled character had disappeared or receded. It was not *lost*, as the next generation showed.

The hybrid offspring, all with rounded seeds, were allowed to self-fertilise. In their progeny roundish seeds and angular wrinkled seeds occurred in the proportions of 3 : 1. Here were the recessives again, and when *they* were allowed to self-fertilise they produced pure recessives only, with angular wrinkled seeds.

The dominants, however, were not all pure dominants, for when they were allowed to self-fertilise they produced one-third pure dominants and two-thirds "impure" dominants, the latter being distinguished by the fact that in their offspring recessives reappeared in the proportion of one recessive to three dominants.

The outstanding facts, taking the case of yellow-seeded and green-seeded peas, may be thus summarised:—

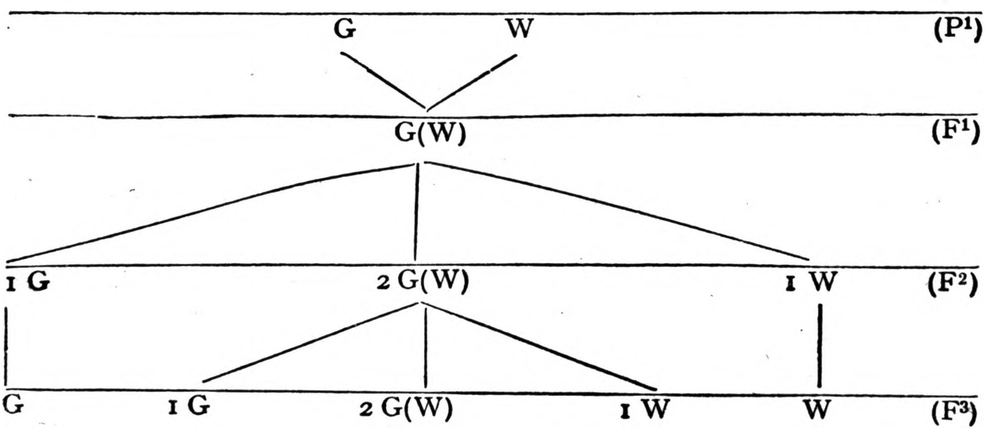
Parental Generation (P1)		Yellow-seeded "pure" plant (dominant)		Green-seeded "pure" plant (recessive)	
First Filial (*Hybrid*) *Generation* (F1)			All the offspring were yellow-seeded. Self-fertilised they yielded		
Second Filial (*inbred*) *Generation* (F2)	Yellows (pure type)		Yellows (impure type)		Greens (pure type)
Third Filial (*inbred*) *Generation* (F3)	Yellows (pure type)	Yellows (pure)	Yellows (impure)	Greens (pure)	Greens (pure type)

Thus intercrossing of forms with contrasted characters results not in transitional blends, but in the dominance of one

character and the recession of another. Self-fertilisation (the extreme of inbreeding) of the hybrids results in a number of pure recessives and a number of dominants in the proportion 1 : 3; some of these dominants (one-third) are pure, and produce only dominants; some (two-thirds) are apparently pure, but produce dominants and recessives in the old proportion, 3 : 1.

A Case of Mice.—Let us take a concrete case from among animals. A grey house-mouse is crossed with a white mouse; the offspring are all grey. Greyness is dominant: albinism is recessive.

The grey hybrids are inbred; their offspring are grey and white in the proportion 3 : 1. If these whites are inbred they show themselves "pure," for they produce whites only for subsequent generations. But when the greys are inbred they show themselves of two kinds, for one-third of them produce only greys, which go on producing greys; while the other two-thirds, apparently the same, produce both greys and whites. And so it goes on.



Summary.—In his exceedingly clear exposition of Mendelism (1905) Mr. R. C. Punnett states the result thus: "Wherever there occurs a pair of differentiating characters, of which one is dominant to the other, three possibilities exist: there are recessives which always breed true to the recessive character;

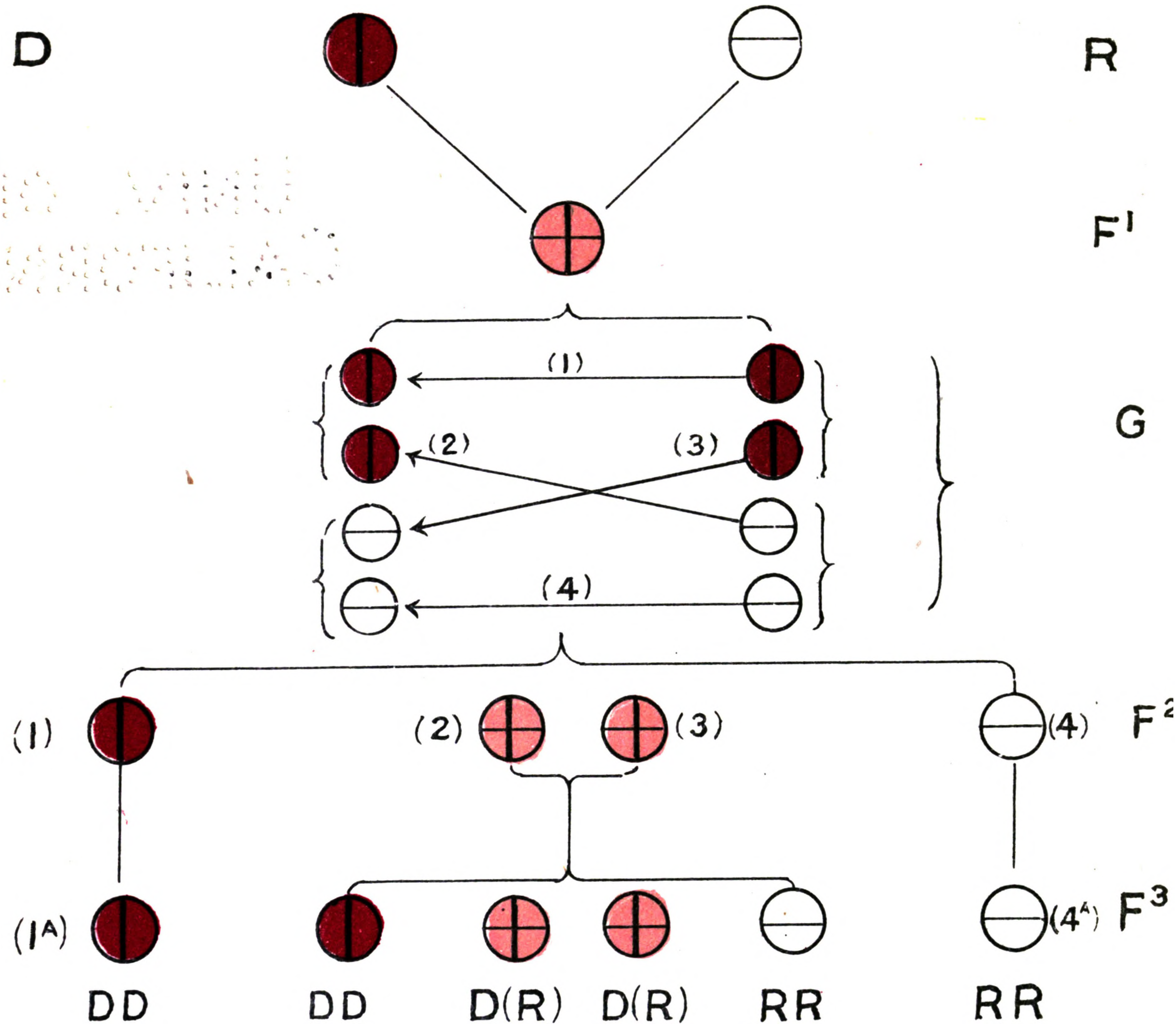


DIAGRAM OF MENDEL'S LAW PARTICULARLY AS ILLUSTRATED IN PROF. CORRENS'S CROSSING OF MIRABILIS JALAPA ROSEA AND MIRABILIS JALAPA ALBA.

FIG. 33.—Diagram showing Mendelian inheritance in Mirabilis jalapa.

D, deep rose parent, *Mirabilis jalapa rosea*; the thick vertical stroke indicates dominance of the deep rose-colour. R, White parent, *Mirabilis jalapa alba*; the thin horizontal stroke indicates recessiveness of the white colour. F^1 Hybrid offspring, light rose D(R). The dominance of the rose was incomplete. G. Germ-cells hypothetically segregated into pure deep rose and pure white; their possible fertilisations indicated by arrows. The male cells are to the right, the female to the left. The fertilisation of two "homozygotes" or similar germ-cells indicated by the arrow (1) yields (1) in the next generation F^2—extracted pure dominant: the fertilisation of two "homozygotes" indicated by the arrow (4) yields (4) in the next generation F^2—extracted pure recessive. The fertilisation of "heterozygotes" indicated by the arrows (2 and 3) yield (2 and 3) in the next generation F^2—impure dominants, which being inbred (self-fertilised) split up in the next generation F^3 into deep rose, light rose, and white as before, in the proportions 1 : 2 : 1. Note also that 1 in the generation F^2 yields a pure dominant 1^A in the third generation F^3; and that 4 in F^2—yields a pure recessive 4^A in the third generation F^3.

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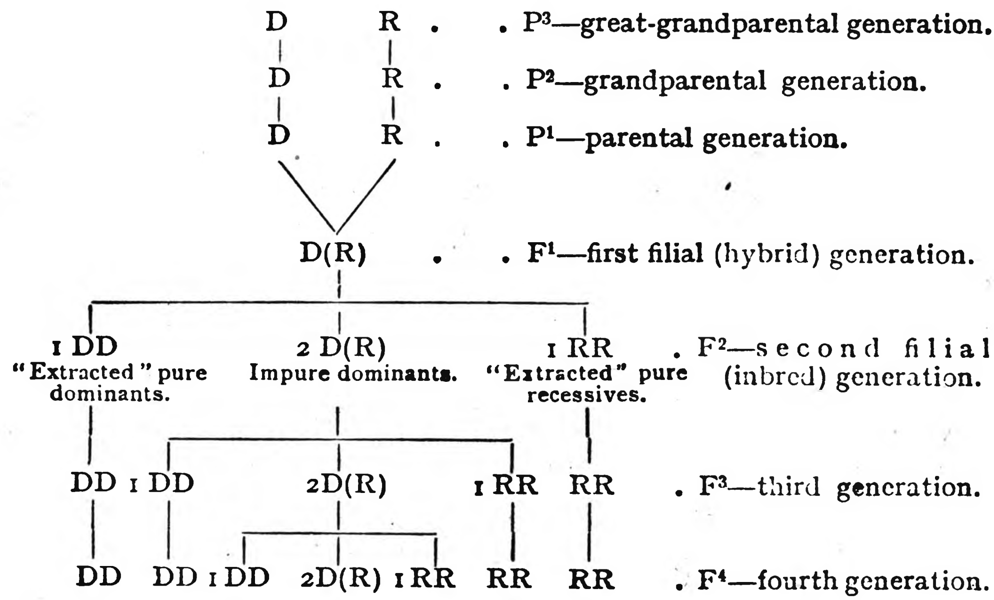
there are dominants which breed true to the dominant character, and are therefore pure; and thirdly, there are dominants which may be called impure, and which on self-fertilisation (or in-breeding, where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter."

Schematic Representation of Mendel's Law.—Following Mr. Punnett's suggestion, with slight modifications, we may use the symbols P^1, P^2, P^3 for the parental, grandparental, and great-grandparental generations; F^1 for the first filial (hybrid) generations; F^2, F^3, F^4 for the subsequent inbred generations. The symbol D(R) means a dominant with the recessive character unexpressed, but potentially present; DD or RR means pure "extracted" dominants or recessives—*i.e.* those pure forms which are sifted out from the inbreeding of "impure" dominants.



§ 2. *Theoretical Interpretation*

Mendel was not content with formulating his results in a law; he advanced a theoretical interpretation which is at once ingenious and simple.

Let us take the case of pea-plants with the quality of tallness or dwarfness, of round seeds or angular seeds, of coloured seed-coats or white seed-coats, of yellow or green cotyledons, or of purple or white flowers (in each case, the *dominant* character has been named first). Let us assume that these are pure-bred varieties, well-established and breeding true, the tall form always producing tall offspring, the dwarf form always producing dwarf offspring, and so on. Let us also assume that the germ-cells contain material representative of these "unit characters"—tallness, dwarfness, rounded seeds, angular seeds, yellow cotyledons or green cotyledons, purple flowers or white flowers.

The egg-cell of the tall pea is normally fertilised by a pollen-grain from the same pea, and the fertilised egg-cell develops into an embryo which becomes a tall pea. As the varieties breed true we assume that the only quality affecting dimensions which the germ-cells bear (*in expressible strength, at least*) is the quality of tallness.

But let us now take the case of a tall pea pollinated from a dwarf pea. The offspring become tall peas—the parent with the dominant character is prepotent. But the fertilised egg-cells which give rise to these tall peas must have contained not only representative primary constituents corresponding to the quality of tallness; but also representative primary constituents corresponding to the quality of dwarfness. This quality of dwarfness is not expressed in development, but it must be present, as subsequent generations show; for when the egg-cells of the hybrids are self-fertilised they develop into offspring partly tall and partly dwarf. What Mendel suggested was that the hybrid produces in equal numbers *two kinds of germ-cells* (two kinds of egg-cells or two kinds of pollen-grains)—that there is in the developing reproductive organ a segregation of germ-cells into two equal camps, one camp with the potential "factor" of tallness, the other camp with the potential "factor" of dwarfness. If there be six ovules, three have in their egg-

cell the primary constituent or factor corresponding to tallness, and three contain the primary constituent or factor of dwarfness. Each of these is pollinated by a pollen-grain, which, by hypothesis, contains the potential quality of tallness or of dwarfness; and if the two kinds of pollen-grains are present in equal numbers, each ovule has an equal chance of being fertilised by a pollen-grain with a potential quality of tallness or by a pollen-grain with a potential quality of dwarfness. *Therefore* the result must be a set of offspring partly dominant and partly recessive, in the proportions of 3 : 1.

A schema will make the theory obvious:

D (*tall*) ♀ × R (*dwarf*) ♂

Egg-cell . ⦶ × ⊖ . Male-cell.

Fertilised egg-cell ⊕ This develops into an organism, whose body-cells express the quality "tallness" (D). The germ-cells of the organism segregate into two sets.

The mature egg-cells consist of two sets; half with the potential quality "tallness," half with the potential quality "dwarfness."

⦶ ⦶ ⦶ ⦶ ⊖ ⊖ ⊖ ⊖

⦶ ⦶ ⦶ ⦶ ⊖ ⊖ ⊖ ⊖

The mature male cells also consist of two sets, with the potential quality of "tallness" or of "dwarfness." What are the chances of fertilisation?

The result must be—

⦶ ⦶ ⊕ ⊕ ⊕ ⊕ ⊖ ⊖

i.e. 2 with the quality of tallness;
4 with the qualities of tallness and dwarfness;
2 with the quality of dwarfness.

In other words—

$$2\,D + 4\,D(R) + 2\,R;$$

or more generally—

$$n\,D + 2\,n\,D(R) + n\,R$$

But as the D(R) offspring are not distinguishable from the D offspring, until further breeding shows that they carry the recessive character in latent form, the proportion is—

3 dominants to 1 recessive.

Thus, Mendel assumed that in the hybrid D(R)—between a parent with a dominant character D and a parent with a homologous recessive character R—the germ-cells segregate into two camps, one half containing the dominant character *in potentia* (d), and the other half containing the recessive character (r). This occurs in both males and females, so that when inbreeding takes place the possibilities are expressible thus :

D(R) produces	50 with (d)	50 with (d)	D(R) produces 100
100 egg-cells	50 with (r)	50 with (r)	sperm-cells

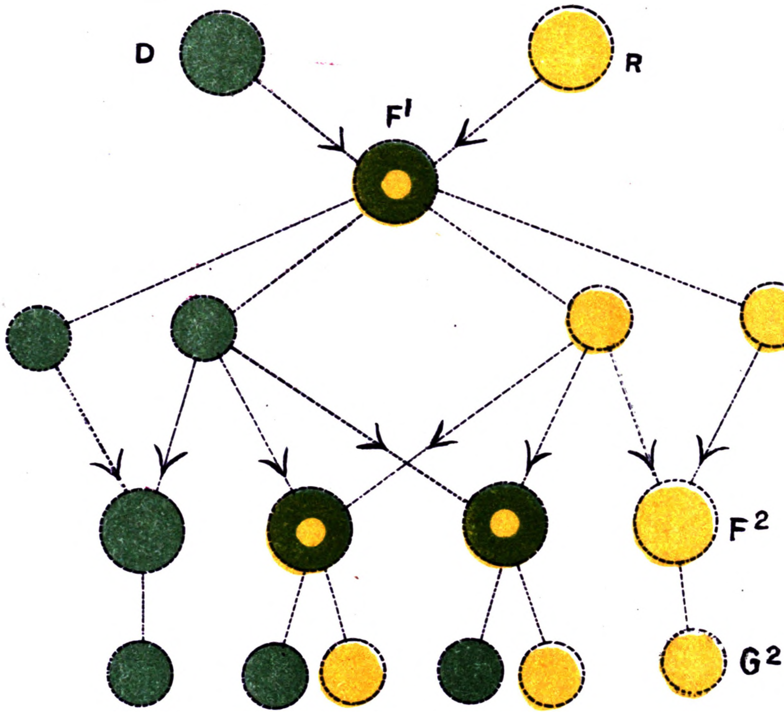
(1) 25 egg-cells (d) fertilised by 25 sperm-cells (d) = 25 fertilised gametes (d).
(2) 25 ,, (d) ,, ,, ,, (r) = 25 ,, ,, (dr).
(3) 25 ,, (r) ,, ,, ,, (d) = 25 ,, ,, (dr).
(4) 25 ,, (r) ,, ,, ,, (r) = 25 ,, ,, (r).

To sum up, 25 (d) developing into 25 pure D.
50 (dr) ,, ,, 50 D(R).
25 (r) ,, ,, 25 pure R.

Bateson has proposed the useful term *homozygous* for individuals in which two like characters have met together (the pure dominants and pure recessives), and *heterozygous* for individuals in which unlike characters have met (the impure dominants).

The Presence and Absence Theory.—One of the root-ideas of Mendelism is that the inheritance includes numerous distinct and independently heritable unit-factors. In certain cases Mendel found that these factors occurred in contrasted or alternative pairs, of such a nature that only one member of any one pair can find full expression in an individual development. The contrasted characters to which the factors give rise are called "allelomorphs," and one is called dominant and the other recessive. These can be distinguished by their behaviour in breeding, but we do not know what the exact nature of the contrast between dominance or recessiveness may be.

In this connection Bateson has proposed a modification of the Mendelian conception which may be called "the presence and



MENDEL'S LAW

FIG. 34.—Diagram illustrating Mendelian segregation of germ cells.

D, dominant parent: R, recessive parent: F^1, hybrid offspring, the recessive character latent; G^1 the germ-cells of F^1, supposed to be segregated in two camps, green and yellow, with dominant and recessive characters. The arrows indicate possibilities of fertilisation. Two greens may combine, producing pure dominant offspring—to the left. Two yellows may combine, producing pure recessive offspring—to the right. Green and yellow may combine, as at the start, yielding impure dominants—green enclosing yellow. G^2; this line indicates the kind of germ cells produced by the second generation F^2.

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absence theory." "It is possible to express all Mendelian phenomena in terms of a simpler system, according to which the allelomorphism may be represented as consisting essentially not in the presence of separate factors for the dominant and for the recessive characters, but in the *presence* of something constituting the dominant character which is *absent* from the recessive gametes." A black guinea-pig is dominant over an albino guinea-pig, all the offspring being black; it is probable that this should be expressed by saying (with Castle) that "a distinctive *something* of the black parent dominates a corresponding *nothing* of the white parent." But it is especially when we pass beyond such simple cases that the advantages of the presence-and-absence conception over the original Mendelian contrast are seen.

It will, of course, be clearly understood that the facts of Mendelian inheritance remain secure, though the interpretation of what is meant by dominance or of segregation itself may have to undergo modification. Thus we may refer to Dr. Berry Hart's independent interpretation (1909) (which Mendelians will not accept) of admitted Mendelian phenomena.

Mendel's Theory summarised.—Mendel discovered an important set of facts, and he also suggested a theoretical interpretation—the theory of gametic segregation. As Mr. Bateson says, "The essential part of the discovery is the evidence that the germ-cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types, and consequently incapable of transmitting the opposite character; that when such pure similar gametes of opposite sexes are united in fertilisation, the individuals so formed and their posterity are free from all taint of the cross; that there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters."

For recent developments of Mendelism the student should consult T. H. Morgan's *Physical Basis of Heredity* (1919). We cannot do more than emphasise a few important propositions.

In the history of the germ-cells there is a conjugation of homologous chromosomes (paternal and maternal) which are subsequently assorted apart in a free or random fashion between the daughter-cells, some maternal chromosomes going to one pole and some to another, and similarly for the paternal chromosomes.

But further investigation is disclosing an increasing number of cases in which free assortment of genes or factors does *not* occur, for many characters keep together in successive generations, instead of assorting freely. This is called "*Linkage*."

Another important fact is "*Crossing Over*," which means that there is often an interchange of blocks of genes between homologous pairs of chromosomes lying close together.

It is practically certain that the genes are arranged in linear order in the chromosomes and definitely spaced.

In the pomace-fly, Drosophila, the number of linkage-groups is the same as the number of chromosomes, and this may be a general fact.

It frequently happens that one species has twice as many chromosomes as a related species, or has one particular chromosome in duplicate as compared with a related species—a very suggestive fact.

A particular gene may be associated with manifold effects. Similar characters—*e.g.* whiteness in poultry—may be produced by different genes. A particular character is often the product of many genes. In short, the whole concept of a gene or hereditary factor is broad and subtle.

Impure Dominants bred with Pure Types.—In the typical cases discussed above, a hybrid form D(R)—an impure dominant —is supposed to be self-fertilised or inbred. The results are according to the formula 1 DD (pure or extracted dominants) + 2 D(R) (impure dominants) + 1 RR (pure or extracted recessives).

But let us suppose the impure dominant or dominant-recessive D(R) to be bred with a pure type—*e.g.* RR (extracted recessive) (in technical phrase, a heterozygote unites with a homozygote). The impure dominant has, by hypothesis, equal numbers of

two kinds of germ-cell—let us say, of egg-cell. The pure type has only one kind of germ-cell—let us say, of sperm-cell. The chances of fertilisation should be as follows:

$n \obar + n \ominus$ egg-cells of impure dominant;
$n \ominus + n \ominus$ sperm-cells of pure recessive:

The result will be

n ova $\obar$ fertilised by n sperms $\ominus$ $= n$ offspring $\oplus$
n ova $\ominus$ fertilised by n sperms $\ominus$ $= n$ offspring $\ominus$

That is to say, equal numbers of impure dominants and pure recessives.

"This is what actually happens on crossing a fowl having a single comb (RR) with one having a heterozygous 'rose comb.'"

Or let us suppose the impure dominant D(R) to be bred with a pure dominant DD:

$n \obar + n \ominus$ egg-cells of impure dominant;
$n \obar + n \obar$ sperm-cells of pure dominant:
The result will be $n \oplus + n \obar$ equal numbers of impure dominants and pure dominants.

"Here again experiment has borne out theory." Therefore, as Mr. Punnett says, "the generalisation known as the principle of gametic segregation may be regarded as firmly established on the phenomena exhibited by plants and animals when strains are crossed which possess pairs of differentiating characters."

§ 3. *Corroborations*

Case of Paired Dominants and Paired Recessives.—A beautiful experiment was made by crossing a variety of pea with *Round* seeds and *Yellow* albumen (a pair of dominant characters) with another variety with angular seeds and green albumen (a pair of recessive characters). The result was offspring all like the dominant parent. These hybrids were inbred, and the results were some *Round* and *Yellow*, some *Round* and green, some

angular and *Yellow*, some angular and green. (The dominants are represented by italics and capitals.)

RY   ag

RY(ag)

Suppose the germ-cells segregate into the four possible kinds (say 100 of each):

(1) 100 RY (2) 100 Rg (3) 100 aY (4) 100 ag	which in inbreeding unite with four similar kinds	RY 100 Rg 100 aY 100 ag 100

What are the possible combinations (it being understood that form and colour represent a *pair* of characters—*i.e.* RR, Ra, etc., are impossible).

(1)	(2)
25 RY × 25 RY = 25 RY	25 Rg × 25 RY = 25 RY (g)
25 RY × 25 Rg = 25 RY (g)	25 Rg × 25 Rg = 25 Rg
25 RY × 25 aY = 25 RY (a)	25 Rg × 25 aY = 25 RY (ag)
25 RY × 25 ag = 25 RY (ag)	25 Rg × 25 ag = 25 Rg (a)
= 100 RY	= 50 RY + 50 Rg
(3)	**(4)**
25 aY × 25 RY = 25 RY (a)	25 ag × 25 RY = 25 RY (ag)
25 aY × 25 Rg = 25 RY (ag)	25 ag × 25 Rg = 25 Rg (a)
25 aY × 25 aY = 25 aY	25 ag × 25 aY = 25 aY(g)
25 aY × 25 ag = 25 aY (g)	25 ag × 25 ag = 25 ag
= 50 RY + 50 aY	= 25 RY + 25 Rg + 25 aY + 25 ag

The characters in brackets may be disregarded, since they behave as recessives to their correspondents. Thus the total is—

225 RY + 75 Rg + 75 aY + 25 ag
or 9 RY + 3 Rg + 3 aY + 1 ag

This actually corresponds with results obtained.

In illustration of the crossing of forms with two pairs of contrasted characters, let us take one worked out by Toyama, concerning two races of silk-moths. The one had white unstriped caterpillars and yellow cocoons; the other had banded caterpillars and white cocoons. Yellow is dominant over white, and striped over unstriped. Thus all the hybrids (F) had striped

caterpillars with yellow cocoons. The germ-cells of the hybrids are, according to hypothesis, of four kinds, which may be represented by the letters (Y = yellow; y = white; G = striped; g = unstriped) YG, Yg, yG, yg.

Now, the possible combinations of these in fertilisation are:

YG with	YG	= YG	=	Yellow Striped
,, ,,	Yg	= YG	=	Yellow Striped
,, ,,	yG	= YG	=	Yellow Striped
,, ,,	yg	= YG	=	Yellow Striped
Yg with	YG	= YG	=	Yellow Striped
,, ,,	Yg	= Yg	=	Yellow unstriped
,, ,,	yG	= YG	=	Yellow Striped
,, ,,	yg	= Yg	=	Yellow unstriped
yG with	YG	= YG	=	Yellow Striped
,, ,,	Yg	= YG	=	Yellow Striped
,, ,,	yG	= yG	=	white Striped
,, ,,	yg	= yG	=	white Striped
yg with	YG	= YG	=	Yellow Striped
,, ,,	Yg	= Yg	=	Yellow unstriped
,, ,,	yG	= yG	=	white Striped
,, ,,	yg	= yg	=	white unstriped

9 Yellow Striped + 3 Yellow unstriped + 3 white Striped + 1 white unstriped.

Toyama's actual results show a very close approximation to the theoretically to be expected results:

Yellow Striped	6,383	individuals,	56·38%
Yellow unstriped	2,099	,,	18·53%
white Striped	2,147	,,	18·96%
white unstriped	691	,,	6·1%

The ratio 9 : 3 : 3 : 1 in 16 is called the normal Mendelian ratio for a "dihybrid cross," where two pairs of contrasted unit-characters are implicated. In each of the four groups making up the 16 there is one individual homozygous, containing units all similar—viz. YG × YG (one of the 9 yellow striped forms), Yg × Yg (one of the 3 yellow unstriped), yG × yG (one of the white striped), and yg × yg (the single pure recessive white unstriped). Any of these four, if mated with an individual like itself, will breed true—a point of great practical importance.

In books that deal with Mendelism in particular (see Bibliography) the reader will find an account of further complications, *e.g.* when the parents differ in three pairs of contrasted unit-characters. These more complicated cases are of great interest to the breeder or cultivator who wishes to know how to combine various excellences in a type that will breed true.

Blue Andalusian Fowls.—When black and white fowls are crossed there sometimes results a blue or Andalusian fowl " with a minute patchwork of black and white." When these are inbred they produce 25% black, 50% blue, and 25% white with black splashes. This splitting-up is characteristically Mendelian, but what gives rise to the " blue " feature is obscure.

The ingenious Mendelian interpretation in the case of the Andalusian fowl is that the black and the splashed white are the pure breeds, and that the blue Andalusian is a peculiar mongrel. We must refer to Mr. Punnett's essay on Mendelism for the interesting theoretical working out of the case, which is exceedingly instructive, since it shows that Mendelian interpretation is feasible even when the hybrid (the Andalusian) is quite distinct from either parent (black or splashed white).

Yellow Mice.—Somewhat similar is the much-discussed case of yellow mice. The yellow is dominant over all other colours, but it is itself quite unfixable. No pure or homozygous yellows can be obtained. When two yellows are mated, two-thirds of the offspring are yellow and one-third some other colour. It has been suggested that the fertilisations which give pure yellow do occur, but that they come to nothing for some unknown reason. Another case, worked out by Baur, is that of a so-called " golden " snapdragon, which is also unfixable. It produces when self-pollinated two-thirds golden offspring and one-third green. And here there is some evidence of the existence of a few feeble entirely yellow seedlings which are not viable.

Compound Allelomorphs.—A differentiating unit character capable of replacing another or of being replaced by another

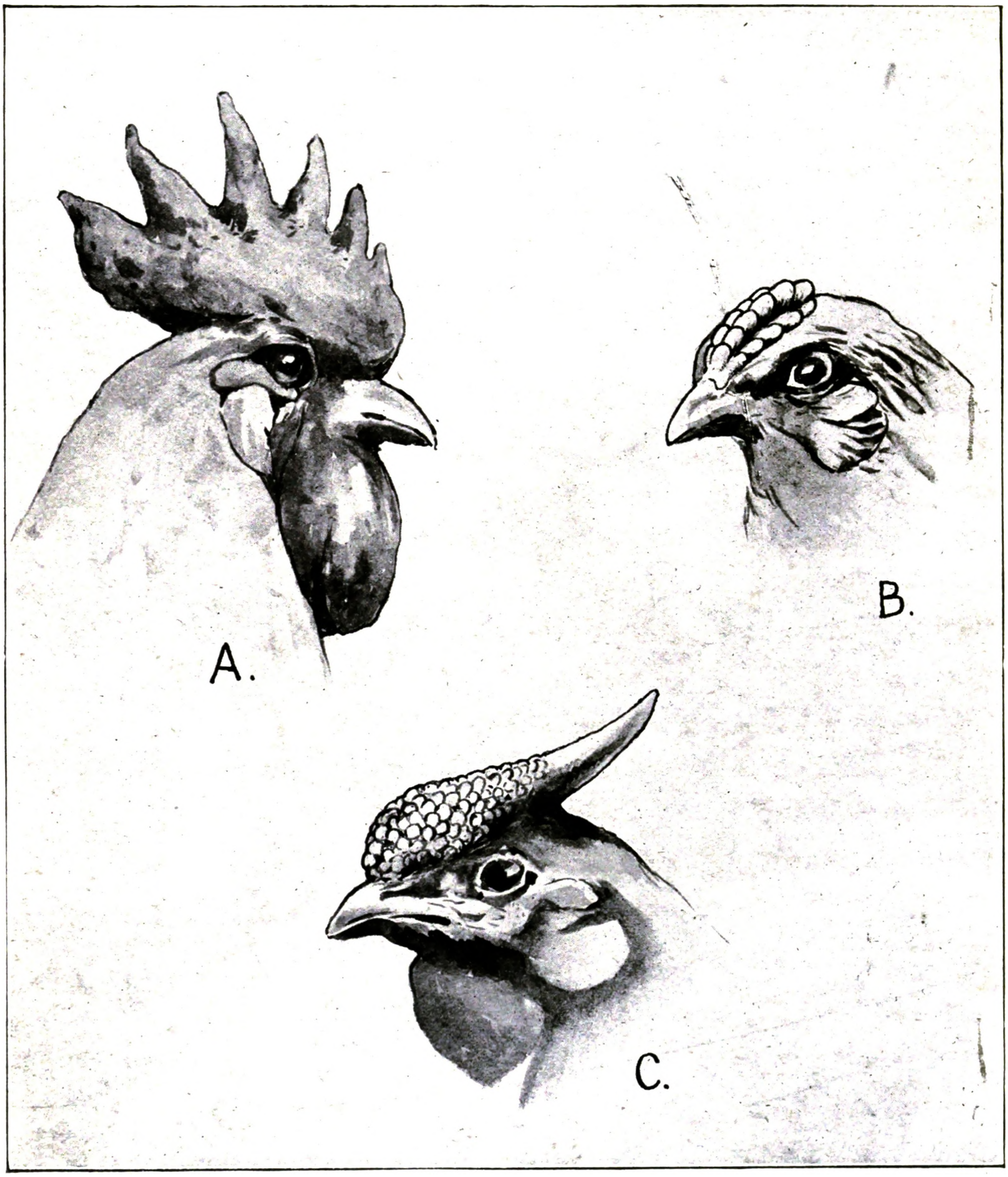

FIG. 35.—Combs of Fowls.

A, Simple serrated comb ; B, Pea comb ; C, Rose comb.

[*Facing p.* 353.

is technically called a *simple allelomorph*. But there are other differentiating characters which seem to consist of several components capable of being isolated and of entering into new combinations. These are called *compound allelomorphs*.

Thus, to take Mr. Punnett's example, the "walnut" comb of Malay fowls—broad, flattened, corrugated like half a walnut, and with small bristle-like feathers posteriorly—becomes, as it were, a compound allelomorph. "This is shown by the fact that it may be synthesised from pure rose and pure pea. It behaves as a dominant to rose, pea, and single * combs. In a zygote formed by the union of walnut with rose or pea the walnut character is stable, and such heterozygotes form an equal number of gametes bearing the walnut, and either the rose or the pea allelomorphs. In other words, the compound allelomorph is stable in the presence of certain presumed simple allelomorphs. When, however, the zygote is formed by the union of walnut with single, the compound allelomorph would appear to undergo partial disintegration with the formation of walnut, rose, pea, and single allelomorphs in equal proportions. The zygote formed by the union of walnut with single is, so far as we at present know, precisely similar to that produced by the meeting of rose and pea" (Punnett, 1905, p. 40).

Sometimes pairs of characters go inextricably together, so that the breeder has not as yet been able to break their correlation. Thus, violet colour and hairiness in *Leucoja* go together, and so do whiteness and baldness in the same flower.

Some very difficult cases are known where the inbred hybrids have progeny some of which resemble one or both of the original parent types, while others resemble quite different types. Thus the Stanley variety of *Lathyrus odoratus*, crossed with the Giant White

* A high serrated "*single*" comb is familiar in Leghorns, etc.; a flattened papillated "*rose*" comb with a posterior pike is seen in Wyandottes, etc.; a low "*pea*" comb, with three well-marked ridges, the median slightly higher than the other two, is characteristic of Indian game-fowl.

variety, yields Giant Purple, which, when inbred, has as progeny Giant White, Giant Purple, Mars, Her Majesty, and a new form.

Mr. Bateson interprets this kind of phenomenon as due to the analysis of a composite character into several sub-characters, while others suppose that latent characters from previous pedigree are liberated by a departure from the usual routine of inbreeding.

Correns has investigated the interesting case of *Mirabilis jalapa*. The white variety, *alba*, crossed with the yellow variety, *gilva*, yields a hybrid with rose flowers and red streaks. When this is inbred the progeny include forms with white, red, rose, yellow, yellowish flowers, with or without various kinds of streaks.

In his important work of 1909, *Mendel's Principles of Heredity*, Professor Bateson wrote: "Of the various cases alleged as exceptional, or declared to be incompatible with Mendelian principles, few have any authenticity. . . . The progress of research has gone steadily to show that facts of heredity which at first seemed hopelessly complicated can be represented in terms of a strict Mendelian system." On the other hand, we find an experimenter like Professor W. L. Tower declaring (1910) that "in the attempt to preserve the letter of the law of Mendelian theory of unit characters with segregation in gametogenesis, a host of hypotheses have been developed in order to save the original theory."

§ 4. *Illustrations of Mendelian Inheritance*

How far has Mendel's Experience been confirmed?—There has been confirmatory work by Correns (on peas, maize, and garden-stock), by Tschermak (on peas), by De Vries (on maize, etc.), by Bateson and his collaborators (on a large variety of organisms), by Darbishire (on mice), by Hurst (on rabbits), by Toyama (on silk-moths), by Davenport (on poultry), and so on. There are some difficulties and not a few discrepancies, but, as Bateson says, "the truth of the law enunciated by Mendel is

now established for a large number of cases of most dissimilar characters."

In experimenting with *Lychnis*, *Atropa*, and *Datura*, Bateson and Saunders found that the phenomena conformed with Mendel's law "with considerable accuracy, and no exceptions that do not appear to be merely fortuitous were discovered. In the case of *Matthiola* (garden stock), the phenomena are much more complex. There are simple cases which follow Mendelian principles, but others of various kinds which apparently do not. The latter cases fall into fairly definite groups, but their nature is obscure."

In experiments with poultry, the phenomena of dominance and recession were detected; interbreeding of the hybrid offspring resulted in a mixed progeny, "some presenting the dominant, others the recessive character, in proportions following Mendel's Law with fair consistency, though in certain cases disturbing factors are to be suspected."

The general result, so far, is that Mendel's Law has received confirmation in a number of very dissimilar cases.

Dominant and Recessive Characters.—Let us first of all collect a number of instances of contrasted characters which behave in relation to one another as dominants and recessives.

	Dominant.	*Recessive.*
	Tallness.	Dwarfness.
Pisum sativum	Round seeds	Wrinkled seeds.
	Coloured seed-coats.	White seed-coats.
	Yellow albumen in cotyledons.	Green albumen in cotyledons.
	Purple flowers.	White flowers.
Sweet pea.	Tall ordinary form.	Dwarf or "Cupid" variety.
	Coloured.	White.
Stocks.	Coloured.	White.
Wheat and barley.	Beardless.	Bearded.
	Later ripening Rivett wheat	Early ripening Polish wheat.
	Non-immune to "rust."	Immune to "rust."

	Dominant.	*Recessive.*
Maize.	" Starch " seed.	" Sugar " seed.
Nettles (*Urtica pilulifera* and *U. dodartii*).	Serrate leaf margin.	Entire leaf margin.
Mirabilis jalapa and *M. rosea.*	Rose colour.	Other colours.
Mice.	Coloured coat. Normal.	Albino coat. " Waltzing " variety.
Rabbits.	Coloured coat. Angora fur.	Albino coat. Short fur.
Poultry.	" Rose " comb of Hamburghs and Wyandottes.	High serrated " single " comb of Leghorns and Andalusians.
Cattle.	Hornlessness.	Horns.
Snails.	Bandless shell.	Banded shell.

Other Instances in Plants.—As is well known, there are two almost equally common forms of wild primrose: (A) thrum-types, with short styles and with anthers at the top of the corolla-tube; and (B) pin-types, with long styles and with anthers half way down the tube. The thrum-type is dominant over the pin-type.

The original species of Chinese primrose (*Primula sinensis*) has a palmate leaf. About 1860 a sport arose (from seed) which had a pinnate or " fern " leaf. The palmate form is dominant, and the fern leaf is recessive.

The deformed " Snapdragon " variety of sweet pea behaves as a recessive to the normal type.

The 2-row barley has certain lateral flowers which are exclusively staminate; in 6-row barley all the flowers are staminate and pistillate, and all set seed. Mr. Biffen crossed these forms, and found that the more negative character was dominant. The offspring were 2-rowed.

Maize.—When the common or starchy round-seeded maize is crossed with the wrinkled-seeded sugar-maize, the round

MIRABILIS JALAPA

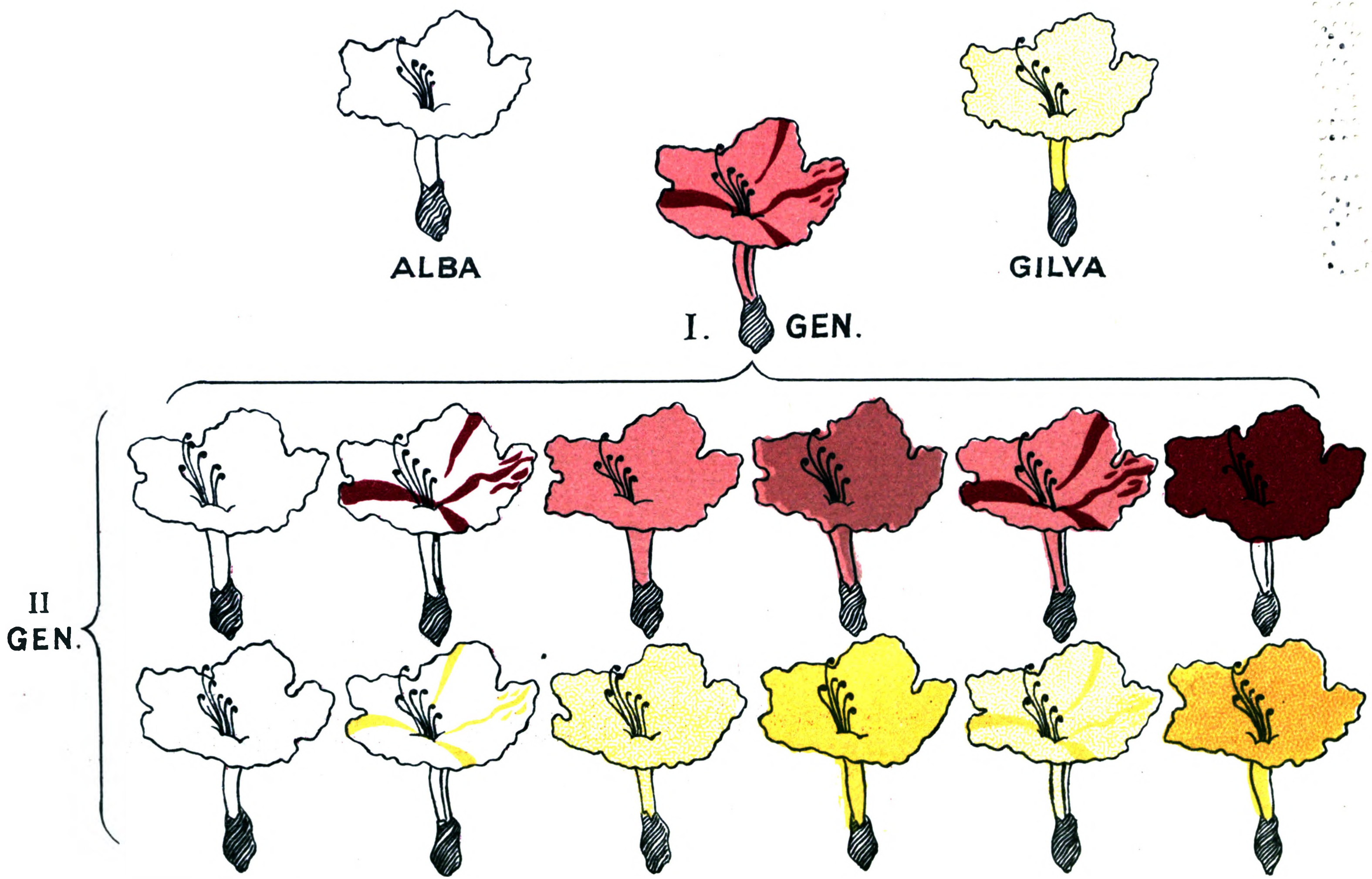

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FIG. 36.—Hybridisation in Mirabilis jalapa. (By kind permission of Prof. C. Correns.) Mirabilis jalapa alba is crossed with Mirabilis jalapa gilva. The hybrid offspring are light rose with red stripes (1. Gen.). When these are self-fertilised there are in their progeny no fewer than eleven kinds of flowers—namely, white, white with red stripes, light rose, deep rose, light rose with red stripes, red, white with yellow stripes, light yellow, yellowish, light yellow with darker stripes, and deep yellow.

[*Facing p.* 357.

starchy character dominates. When an egg-cell of the wrinkled sugar-maize stock is fertilised by a pollen-cell of the round starchy stock, the result is a round seed with starchy endosperm. If this seed is sown, it becomes a plant which, on self-fertilisation, forms a cob with a mixture of round starchy and wrinkled sugary seeds in the ratio 3 : 1. The wrinkled seeds yield sugar-

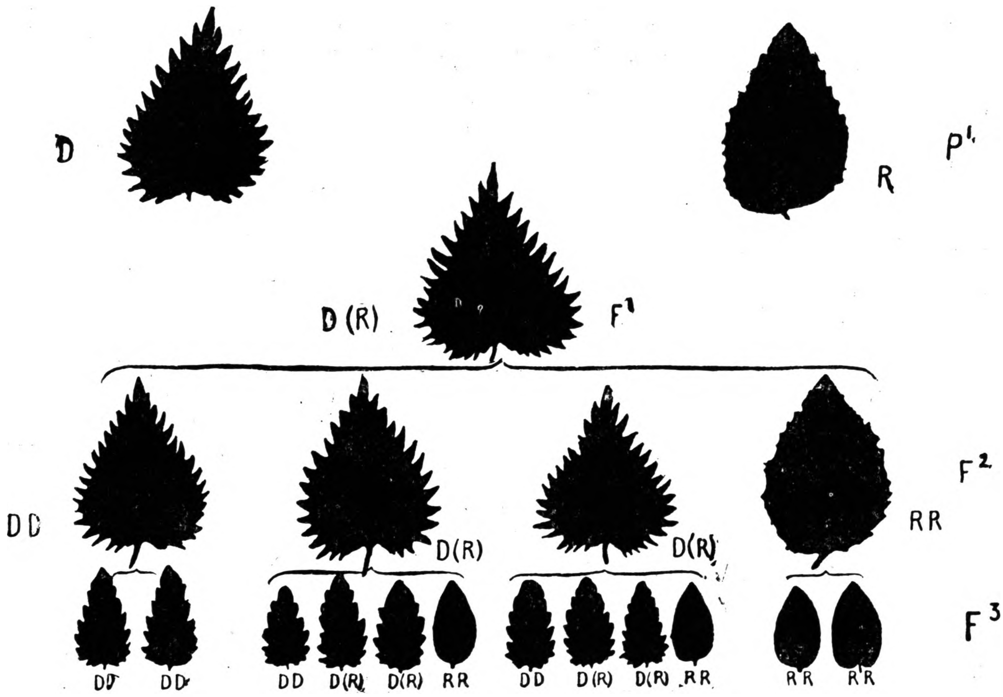

Fig. 38.—Diagram showing Mendelian phenomena in nettles. (By permission of Prof. Correns.)

P^1, leaves of the two parents; D, Urtica pilulifera; R, Urtica dodartii; F^1, leaf of the progeny, D(R), the serrated type being dominant; F^2, leaves of the hybrid's offspring; 1DD + 2D(R) + 1RR; F^3, leaves of the next generation; DD, pure extracted dominants; RR, pure extracted recessives; D(R), impure dominants.

maize; the round seeds yield two "impure rounds" to one "pure round." Correns has observed a very interesting case in which two pairs of contrasted characters are implicated.

One variety, *Zea mays alba*, which has *smooth* white seeds, was crossed with another variety, *Zea mays coeruleodulcis*, which has wrinkled *blue* seeds. The hybrids (F^1) had *smooth*

blue seeds, one character of each parent being dominant, and one character of each parent being recessive. The hybrids were inbred, and the progeny (F^2) showed four combinations—*smooth blue, smooth* white, wrinkled *blue,* and wrinkled white (the dominant characters are italicised).

In the next generation (F^3), the wrinkled white, inbred, yielded wrinkled white—a case of extracted recessives breeding true. The *smooth* whites and wrinkled *blues,* inbred, yielded partly forms like themselves and partly wrinkled white. The *smooth blues,* inbred, yielded the same combinations as in F^2.

A finer corroboration of Mendelism could hardly be wished.

Nettles.—Correns crossed two "species" of stinging-nettle, *Urtica pilulifera* L. and *U. dodartii* L., which resemble one another except as regards leaf-margin, strongly dentate in the former, almost entire in the latter. The hybrid offspring (F^1) have all dentate leaves like the male or the female parent, as the case may be. The dentate character is absolutely dominant. The inbred (self-fertilised) hybrids produce offspring (F^2) of two kinds, with dentate and with entire margins, on an average in the Mendelian proportion, 3 : 1.

Immunity to Rust in Wheat.—Some kinds of wheat are very susceptible to the fungoid disease known as "rust"; others are immune. The quality of immunity to rust is recessive to the quality of predisposition to rust.

"When an immune and a non-immune strain are crossed together the resulting hybrids are all susceptible to 'rust.' On self-fertilisation such hybrids produce seed from which appear dominant 'rusts' and recessive immune plants in the expected ratio of 3 : 1. From this simple experiment the phrase 'resistance to disease' has acquired a more precise significance, and the wide field of research here opened up in this connection promises results of the utmost practical as well as theoretical importance. To the question, 'Who can bring a clean thing out of an unclean?' we are beginning to find an

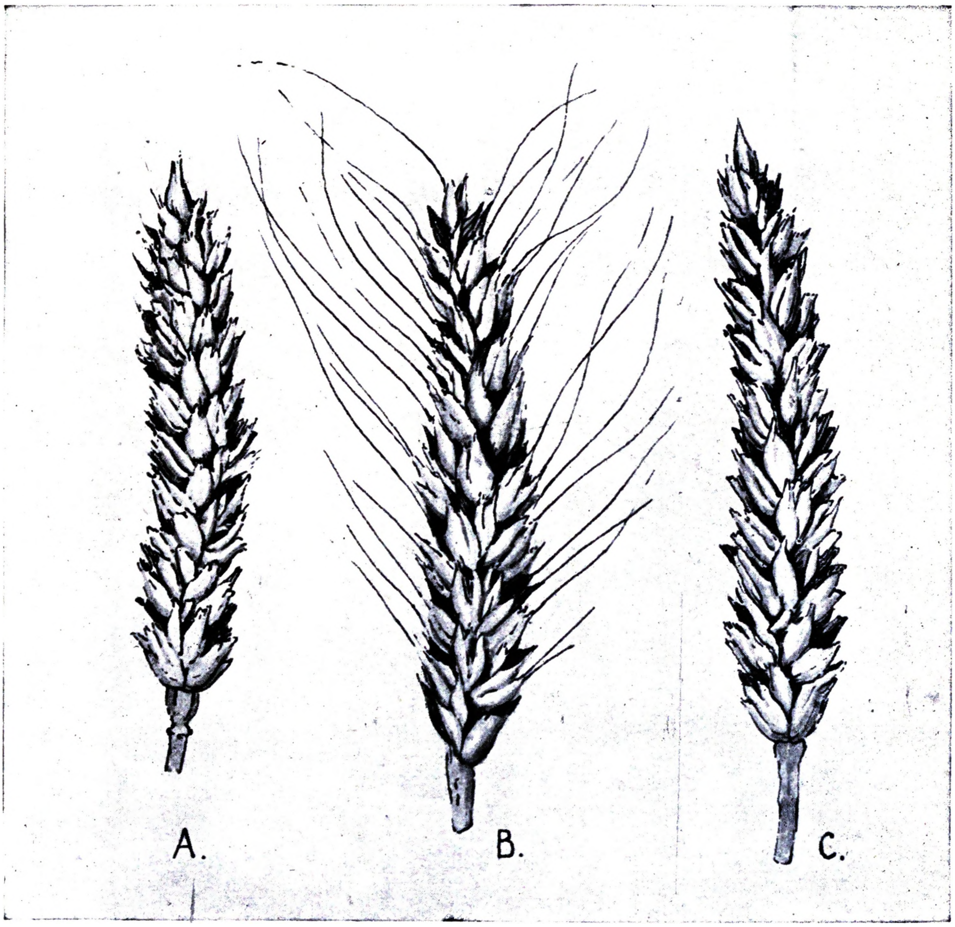

FIG. 38.—Mendelian phenomena in wheat. (After R. H. Biffen.)

A, Stand-up wheat; B, Bearded wheat; C, The hybrid, showing that the beardless condition is dominant over the bearded.

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answer, nor is the answer the same as that once given by Job" (R. C. Punnett, 1905, p. 18).

Silkworms.—Toyama paired Siamese silkmoths, with yellow or with white cocoons; the offspring produced only yellow cocoons. When the hybrids were inbred, the result was two sets, one producing white cocoons, the other producing yellow cocoons, and the proportion was Mendelian—25·037 white and 74·96 yellow. The whites bred true; the yellows when inbred showed themselves to be pure dominants or "yellows" and dominant-recessives—*i.e.* splitting up again into yellows and whites in the usual proportion. More intricate experiments confirmed this general result.

It must be noted, however, that Coutagne has made much more elaborate experiments with different results, which in *many* cases cannot be interpreted on the Mendelian theory. Thus he found (1) that the hybrid forms were sometimes blends of the parents and different from both; (2) that in other cases the brood included some like one parent in a particular character, some like the other parent, and some intermediate; and (3) that in other cases the individuals showed no fusion of characters, but resembled one or other parent. It is likely that the discrepancy may be explained as due to considerable diversity of origin in the domesticated races of silkworm, so that, while they breed true when left to themselves, a disturbance of the usual routine leads to the liberation of latent characters.

Lina lapponica.—Miss McCracken has made a fine study of the hereditary relations in this Californian beetle, which occurs in two types, spotted (dominant) and black (recessive). They are always crossing in natural conditions, but there are no intermediates, and it is easy by isolation to rear a "pure" spotted race and a "pure" black race. When spotted forms are paired they may produce only spotted progeny—a case of extracted dominants. In other cases, however, they yield spotted and

black forms (1,021 spotted, 345 black), *i.e.* in the Mendelian proportion of 3 : 1—a case of dominant-recessives inbred.

Snails.—Lang paired "pure" five-banded forms of the common or garden snail, *Helix hortensis*, with bandless forms from bandless colonies. The young of the first generation were all bandless, the banded character being recessive. When these were paired the offspring were bandless and banded in the Mendelian ratio, 3 : 1. Further experiments confirmed this, not only as regards bands, but also as regards colour (yellow or red), size, and the form of the umbilicus. *It may be said, therefore, that common snails* (*Helix hortensis* and *Helix nemoralis*) *illustrate Mendelian inheritance.*

Poultry.—Numerous breeding experiments with poultry have been made by Bateson, Bateson and Punnett, Hurst, Davenport, and others, many of which show Mendelian phenomena with great clearness, while others are strangely conflicting. One of the reasons for the complicated results is evidently to be found in the difficulty of securing thoroughly "pure" breeds, for many that breed true as long as they are inbred tend to liberate latent characters when the ordinary course of breeding is departed from.

Hurst contrasts the following characters, which usually show themselves dominants and recessives; but it has to be admitted that the dominance—always complete for some characters—is for others frequently, or even always incomplete—*i.e.* showing traces of the corresponding recessives.

Dominant Characters.	*Recessive Characters.*
Rose comb.	Leaf comb, single comb.
White plumage.	Black plumage, buff plumage.
Extra toes.	Normal toes.
Feathered shanks.	Bare shanks.
Crested head.	Uncrested head.
Brown eggs.	White eggs.
Broodiness.	Non-broodiness.

Davenport's copiously illustrated work is also of great interest. He shows in case after case that the character dominant in the

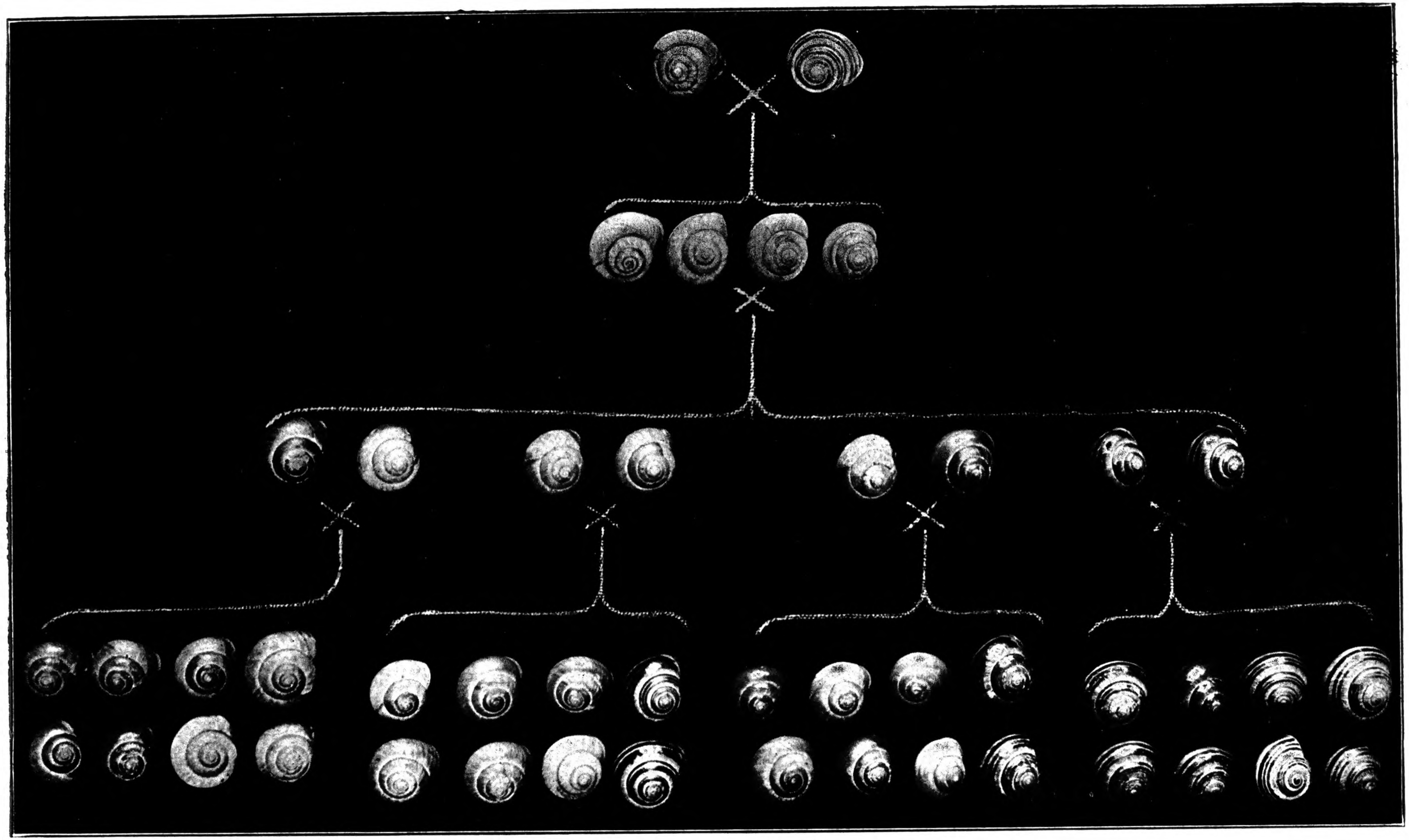

FIG. 39.—Diagram to illustrate Mendelian phenomena in *Helix hortensis*. (After Lang.) The diagram was photographed from random shells, not from the real subjects of experiment, as in Lang's figure.

The first line shows a bandless (D) and a banded (R) form; the bandless form is dominant; the second line shows (F^1) four bandless forms D(R); the third line shows (F^2) the progeny of the hybrids, 6 bandless and 2 banded 1D+2D(R)+1R; the fourth line (F^3) shows pure extracted bandless dominants to the extreme left, pure extracted banded recessives to the extreme right, in the middle two groups of 3D+1R.

[*Facing p.* 360.

first hybrids is more or less influenced by the recessive character. Polish fowls with a large hernia of the brain on the top of the head were paired with Minorcas with normal heads. The hybrids showed no hernia, but most of them showed a frontal prominence. When the hybrids were inbred the hernia occurred in 23·5%—a close approximation to the theoretical 25%.

Single-combed black Minorcas were crossed with white-crested black Polish fowls with a very small bifid comb. The hybrids had combs single in front, split behind. When the hybrids were inbred there resulted in a total of 101 offspring, 29·7% with single combs (like Minorcas), 46·5% with Y-shaped combs, and 23·8% with no combs or only papillæ (like the Polish forms). Here, again, the result is in a general way Mendelian, but the Y-like comb is a complication.

Pigeons.—R. Staples-Browne crossed a web-footed pigeon (an occasional discontinuous variation) with a normal form, and got six normal young. In other words, the web-foot character is recessive to the normal foot character. The hybrids were inbred, and in one case produced nine with normal feet and three with webbed-feet—a Mendelian splitting-up. But from another pair of hybrids seventeen normal offspring resulted. Thus, the illustration of Mendelian inheritance is inconclusive. Besides, the numbers were too small.

We have noticed elsewhere that crossing different breeds of pigeons often results in forms which more or less resemble the reputed original ancestor, the wild rock dove; in other words, reversions occur. Often, however, the results seem quite anomalous, which is probably due to the number of latent characters which different races of pigeons appear to carry.

Mice.—Mendelian phenomena have been carefully studied in mice. Thus, when a grey mouse is paired with an albino, the hybrid offspring are always grey. When these are inbred, they yield greys and albinos, approximately in the proportion 3 : 1. Thus Cuénot obtained 198 greys and 72 albinos.

Darbishire has obtained many results which harmonise well with Mendelian theory, while others require some ingenuity if they are to be fitted in with this interpretation. As a good case we may cite one where the inbreeding of pigmented mice—derived from crossing pigmented and albino individuals—yielded 159 pigmented young and 55 albinos (53·5 being the theoretical anticipation). When similar hybrids were paired with pure albinos, they yielded 69 pigmented and 69 albino forms, precisely as the theory would lead us to expect:

D R

D(R)
×
D(R)

1 D + 2 D(R) + 1 R
×
2R

D(R) R

Cuénot crossed an albino *A*G (with latent grey) with an albino *A*B (with latent black), and obtained albinos (*A*G*A*B). He crossed a black mouse C*B* with an albino *A*Y (with latent yellow), and obtained yellow mice (CBA*Y*). He then paired *A*G*A*B (albino) with CBA*Y* (yellow) and obtained 151 young—81 albinos, 34 yellow, 20 black, 16 grey; the theoretical anticipation being—76 albinos, 38 yellow, 19 black, 19 grey. This is an exceedingly striking and convincing case.

Waltzing Mice.—The mice of this interesting Japanese breed have among other peculiarities the habit of waltzing round in circles. When waltzing mice are crossed with normal mice, their abnormal quality behaves as a recessive.

Guinea-pigs.—If a black guinea-pig of pure race be crossed with a white one the offspring will be all black, and if these are mated with each other the recessive white character reappears

on the average in one in four of their offspring. These whites mated with each other produce only white offspring, while the black are as usual of two kinds, pure blacks and impure blacks Similarly, as Professor Castle has shown, a rough coat is dominant over a smooth coat, and a short coat over a long coat.

Rabbits.—Hurst paired white Angora rabbits (with pink eyes and silky hair) with "Belgian hare" rabbits (with pigmented skin, dark eyes, and short yellow fur). The hybrids were pigmented like the "Belgian hares," but the fur was grey like that of the wild rabbit. These hybrids were inbred, and 14 distinct types resulted—an apparent "epidemic of variation" to which Mendel's theory has supplied the clue, for four pairs of contrasted characters are involved in the hybrid inbreeding—namely, short hair versus long hair, pigmented coat versus albinos, grey versus black coat, uniform versus marked coat (Dutch marking latent in the albinos), and the 14 distinct types illustrate the possible combinations.

As regards short hair versus long hair, Hurst found that when the short-coated hybrids were inbred they produced short-haired forms like the Belgian hare grandparent, and long-haired forms like the Angora grandparent. Out of 70 which reached the age of two months or more, 53 were short-haired and 17 long-haired—a close approximation to the Mendelian anticipation, 52·5 : 17·5. Similarly, as regards pigmented coat versus albino, the hybrids, when inbred, yielded 132 pigmented and 39 albino forms—a close approximation to the Mendelian expectation, 129 : 43; and so on.

Cats.—There are some interesting results as to colour (Doncaster). Thus, "pure" orange ♀ crossed by "pure" black ♂ gives tortoiseshell females and yellow males, but black ♀ crossed by orange ♂ gives black males or females, tortoiseshell females, and orange males. It seems that orange usually dominates over black in males, while in females the orange (for some unknown reason) is less dominant and tortoiseshell results. Male tortoise-

shell-cats are very rare. In this case, the results are complicated by some peculiarity wrapped up with "sex."

When a male tortoiseshell is paired with a female tortoiseshell the kittens are tortoiseshell, orange, and black—which is what Mendelian theory would lead us to expect.

Man—The evidence of Mendelian phenomena in man is accumulating. It appears that the condition known as brachydactylism, where the fingers are all thumbs with two joints instead of three, is dominant over the normal. In five generations chronicled by Farabee about half of the offspring were of the abnormal type, though the marriages were apparently always with unrelated normal individuals. Moreover, no normal member of the lineage is known to have transmitted the abnormality. Another good case has been recently discussed by Drinkwater.

Of great interest also is Mr. Nettleship's account of the descendants of one Jean Nougaret (born 1637), who was afflicted with "night-blindness"—a condition apparently due to loss of the visual purple. It seems to behave like a unit character. There are records of over 2,000 individuals; and the night-blindness is dominant over normal eyesight. The notable point is that during two and a half centuries no normal member of the lineage who married another normal, whether related or not, ever transmitted the disease.

Human eye-colour affords another illustration. It is largely determined by the presence or absence of two distinct layers of pigment. "In the true blue eye only one of these pigmentary layers is visibly present, the posterior purple pigment of the choroid, which, being reflected through the fibrous structure of the iris, produces the blue colour. In the absence or partial absence of this pigment the eye appears to be "pink," as in albinos. In the ordinary brown eye two layers of pigment are present, for in addition to the posterior purple layer there is also an anterior brown layer, in front of the iris. Major C. C.

Hurst found that the eye with two layers of visible pigment (duplex) is dominant and the eye with one layer of visible pigment (simplex) recessive. Or, putting it in another way, the presence of the brown front layer is dominant to its absence. Practically the same conclusion was reached independently by Professor and Mrs. Davenport.

The Davenports and Major Hurst have also brought forward some evidence illustrating in typical Caucasians the dominance of dark to fair skins, their segregation in the same family, and the apparent purity of the extracted fair individuals. Hurst also gives evidence that "fiery red" hair behaves as a recessive to brown, and that the musical sense or temperament is also recessive. It seems as if an individual is non-musical owing to the presence of an inhibitory factor preventing the expression of the musical temperament which is potentially present in every one (Hurst, 1912).

It would be interesting to have precise information as to the progeny of Eurasians who intermarry, for here the original hybrids result from the mixture of two very distinct races.

§ 5. *Mendel's Discovery in Relation to Other Conclusions*

Conception of the Organism.—A keen critic has pointed out that the Darwinian or Selectionist theory of evolution is obviously a projection on nature of anthropomorphic ideas partly due to the keen competition of the industrial age, partly due to a temporary pressure of over-population, partly due to the process by which mechanical devices, such as spinning and weaving machinery on the one hand and bicycles on the other, are improved by the addition of one patent after another. Taking the last point, the critic asks if we can seriously believe that organisms have evolved by piecemeal variation and selection of particular parts, comparable to improvements now in the gear, again in the steering, and again in the chain of the bicycle? Is it not one

of the clearest and surest facts about an organism that it is a unity? It lives as a unity, does it not evolve as a unity?

We cannot here enter into a discussion of the alleged anthropomorphism or sociomorphism of what we flatter ourselves by calling "pure science." That is a very interesting thesis, and worthy of much discussion. But we wish to refer for a moment to the idea of the "piecemeal patenting theory" of evolution, since it seems to us that the *facts* brought to light by Mendel and the Mendelians are sufficient to show that there is some truth in this way of looking at the organism.

It has been shown that some organisms have clear-cut, we may almost say crisp, unit characters, which behave in inheritance as if they were independent constituents, being transmissible *en bloc* and in their entirety—not blending with analogous characters, but remaining quite distinct, and developing in absolute intactness and exclusiveness or not at all.

The Mendelian facts, as Bateson says, lead us to regard the organism as "a complex of characters, of which some at least are dissociable and are capable of being replaced by others. . . . We thus reach the conception of unit characters, which may be rearranged in the formation of the reproductive cells. It is hardly too much to say that the experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the atomic laws of chemistry."

Weismann has not paid much attention to Mendel's Law, because he regards the basis of facts as still insufficiently broad, and because he sees so many discrepancies in the experimental results; but it may be pointed out that the general idea of independently heritable unit characters is not inconsistent with, but rather corroborates Weismann's picture of an inheritance as composed of numerous sets of determinants or primary constituents, each corresponding to an independently variable and heritable structure. It is quite possible that the germ-cells of the hybrids of two distinctively contrasted parents do not separate

into two sets bearing "pure" dominant determinants and "pure" recessive determinants, but that the practical "purity" is wrought out by a process of germinal selection.

However this may be, the facts of Mendelism lead us to a renewed confidence in the relative independence of unit characters. It looks as if a unit character sometimes behaves like a radicle in chemistry; it can be replaced *en bloc* by another, but it cannot compromise with that other. "The outlook," as Bateson says, "is not very different from that which opened in chemistry when definiteness began to be perceived in the laws of chemical combination."

A New View of Evolution.—As is well known, Darwin believed that specific differences and adaptations were slowly brought about by the consistent selection of small continuous variations in a profitable direction. He did, indeed, recognise that large discontinuous variations may suddenly arise, as in the case of the short-legged Ancon sheep. He could not, however, lay stress upon such occurrences, believing as he did that they were of rare occurrence, and therefore very liable to be swamped by intercrossing with the normal forms.

Over and over again, both before and after Darwin, naturalists had suggested that sudden emergences of new structures with no small degree of completeness, brusque transitions from one position of organic equilibrium to another, might be of evolutionary importance. We need only mention Etienne Geoffroy Saint-Hilaire and Francis Galton. But the difficulty always was, that these discontinuous variations seemed to be of rare occurrence, and liable to be swamped.

In 1894 Bateson showed in his *Materials for the Study of Variation* that discontinuity in variation was a fairly common phenomenon, and might, therefore, have played in the past an important rôle in the origin of species (see Chapter III.).

Similarly, Hugo de Vries showed in most convincing detail that sudden discontinuous variations or mutations not infre-

quently occur among plants and give rise to true-breeding varieties (see Chapter III.).

Now it is evident that, if Mendel's Law applies in such cases, the mutation, once present, is not likely to be lost or swamped by inbreeding with the normal types. Thus, through Mendel's discovery we are led to a new view of organic evolution, in which we attach less importance to the minute fluctuations on which Darwin relied, and more importance to mutations or saltatory variations.

Light thrown on Variation.—Mendelian experimentation has thrown light on at least some kinds of variation. In connection with the colours of flowers and of the coats of mammals, it has been shown that varieties may arise by the loss or modification of unit-characters. Thus in the case of a rabbit, some colour-factor may drop out altogether, giving albinos, or the pattern-factor of the individual hairs may drop out, giving a mingling of pigment which appears black, or the factor for black may drop out, giving brown and cinnamon varieties. But what does this "dropping out" mean? Prof. Castle answers: "Loss of a unit-character might easily come about by an irregular cell-division in which the material basis of a character failed to split, as normally. . . . On the other hand, a modified condition of a unit-character might possibly result from *unequal* division of the material basis of a character, so that one of the cell-products would transmit the character in weakened intensity, the other in increased intensity" (1911, p. 86).

Some Mendelians would also admit the idea that a unit-character may lose some of its "potency," some of its power of "dominating" or of asserting itself in development—just as it might on Weismann's theory of germinal selection. We have already referred to the not infrequent imperfection of the dominance of a dominant character. It may be that this is due to a weakening of the potency of a particular unit-character; it may be that something must be allowed for the condition of the

entire germ-cell at the time of fertilisation. Prof. W. L. Tower, in a series of important experiments testing the influence of altered environmental conditions on the breeding of potato-beetles (*Leptinotarsa*), found that the conditions surrounding and incident upon the germ-cell at the time of fertilisation may be to a very considerable extent responsible for the determination of the dominant character in the cross and largely responsible for the variability of such characters (1910, p. 332).

Mendelian experiments give us a vivid impression of the possibilities of variation. Crossing two races of silk-moth, one with striped caterpillars and yellow cocoons, the other with unstriped caterpillars and white cocoons, yields in the hybrid generation (F^1) only forms with striped caterpillars and yellow cocoons, these being the two dominant characters. But the inbreeding of the hybrids yields in the next (F^2) generation, four different combinations which we may briefly allude to as—Yellow Striped, Yellow unstriped, white Striped, and white unstriped. But if there had been 10 unit-characters instead of four, there would have been a theoretical possibility of 1,024 combinations. In short, Mendelism enables us to understand the origin of that kind of variation which consists of permutations and combinations of already existing qualities.

Mendelism in Relation to Selection.—The facts of Mendelism are in several ways important in relation to natural selection :—(1) The facts warrant us in believing in the possibility of the particular evolution of unit characters while the rest of the organism remains stable. (2) When a variation is, through inherent stability or through inbreeding, prepotent—*i.e.* when its possessors breed true *inter se*—we can understand how it is that even crossing with variants having an antagonistic character need not imply any diminution of the dominance of the character in question. The inbreeding of the hybrids simply results in the sifting out of the pure parental types. (3) Suppose Mendelian phenomena to occur in a series of generations, and suppose

that natural selection favours the possessor of the dominant character, they will *ex hypothesi* prevail as elimination proceeds. But it should also be noted that, apart from selection, the possessors of the dominant character will be in a gradually increasing majority, since extracted dominants and dominant-recessives (practically indistinguishable as far as natural selection goes) are always to recessives in the proportion of 3 : 1.

In the beautiful case of the two nettles given by Correns, the plants with entire leaf-margins are markedly more susceptible to fungoid attacks than those with dentate margins, so that in the course of time in certain conditions the former race would tend to be eliminated by natural selection ; but it is also handicapped by the hereditary conditions, since three dominants are always being produced to one recessive.

Swamping Effects of Intercrossing.—A well-known objection to Darwinism, first clearly stated by Prof. Fleeming Jenkin, is that variations of small amount and sparse occurrence would tend to be swamped by intercrossing before they had time to accumulate and gain stability. In artificial selection the breeder takes measures to prevent this "swamping-out," by deliberately pairing similar or suitable forms together, or by deliberately removing undesirable forms ; but what, in nature, corresponds to the breeder ?

Various answers are possible :—(1) It may be that similar variations occur in many individuals at once and many times over. (2) It may be that the variations which really count in evolution are not small individual fluctuations, but discontinuous variations. (3) It may be that many variations are not from the first unstable, but express changes of organic equilibrium which come to stay if they get a chance at all. (4) There are numerous conditions in nature—summed up in the concept "isolation"—*e.g.* geographical barriers, differences in habit, psychical likes and dislikes—which tend to prevent free intercrossing between sections of a species. Similar forms

may pair, and, in various ways, assortative mating may come about naturally. And whenever inbreeding sets in prepotency develops—*i.e.* peculiarities, even if trivial, gain great staying-power in inheritance. (5) But even more important are the facts disclosed by Mendel and his school, that crossing does *not* tend to swamp new features, for if the hybrids be inbred there is a persistent segregation of the parental type. A new mutant crossed with a related form of contrasted character may be dominant or recessive in the immediate hybrid (F^1), but in either case, if the hybrids are inbred, it will reappear in pure form in the next generation (F^2), and so forth. Mendelian experiments show the possibilities of arriving at novelties by combinations of unit-characters, and it is interesting here to refer to the extreme view of Lotsy (see p. 604) that all new races arise by hybridisation.

Mendelian and Statistical Methods.—There seems no sound reason for pitting these two methods against one another. In his *Modes of Research in Genetics* (1915), Dr. Raymond Pearl writes as follows: "Hereditary differences behave, in the main, as discrete units, which are shuffled about and re-distributed to individuals, in the course of the hereditary process, to a considerable extent independently of each other." Statistical or biometric methods study the distribution of the hereditary differences in one way, Mendelian methods in another. "The biometric method studies the ancestry of the individual, while the Mendelian method studies the individual's progeny. One goes backward on the pedigree; the other goes forward. The network of descent may be likened to two pencils of light rays both of which focus in the individual. The ancestral pencil converges upon the individual. The progenial pencil diverges from the individual." "The statistical method is a logically necessary adjunct to the experimental method."

When we pass, however, from biometric methods in general to particular formulations, such as Galton's Law (see p. 328), we have to recognise that blending inheritance and Mendelian or alternative inheritance cannot be forced into one generalised statement, and that the Law of Ancestral Inheritance really

applies only to the former, though Galton sought to make it include both.

More generally it may be said that there should not be any opposition between Mendelian and biometric formulæ, for that is a confusion of thought. Biometric formulæ are applicable to averages of successive generations breeding freely; Mendelian formulæ are applicable to particular sets of cases where parents with contrasted dominant and recessive characters are crossed and their hybrid offspring are inbred. We may refer to the admirable essay by Darbishire (1906).

Summary of Mendelism.—The Mendelian theory implies three main ideas.

(1) The inheritance consists, in part at least, of "unit-characters" which are typically continued as a whole or not at all, which behave as if they were discrete units which can be shuffled about and distributed to the offspring to some degree independently of each other. These "unit-characters" are believed to be represented in the germinal material, and probably in the chromosomes, by differential features of some sort—the so-called factors, determiners, or genes. It may be, however, that several factors may be involved in one character, or that one factor may influence more than one character.

(2) When two parents differ in respect to two contrasted unit-characters these do not blend in the offspring, but one of them appears, more or less in its entirety, and is called dominant, while its analogue, that drops more or less out of sight for the time being in the offspring, is called recessive. Or the presence of a character may be dominant to its absence, and conversely. It must be carefully noticed, however, that there are numerous instances of what is called incomplete dominance, as when the crossing of a black and a white Andalusian fowl yields blue Andalusians. Moreover, different pairs of factors may interact, and there are many complications now known which explain how certain distributions of qualities which seem non-Mendelian at first sight, may yet come under that interpretation.

(3) The third idea is that of segregation, that in the history of the germ-cells of Mendelian crosses (the first filial generation), there is a segregation of the factors of, say, two contrasted unit-characters, or of the factors of a unit-character possessed by only one of the parents, the segregation being such that each germ-cell, whether ovum or spermatozoon, is "pure" as regards the character in question, either having or not having the corresponding factor.

Of great interest is De Vries's evidence that certain mutations, involving Mendelian unit-characters, are associated with *chromosome-changes*. In his "Mutation Factor in Evolution" (1915) Ruggles Gates shows in circumstantial detail that peculiarities marking the various mutants of the Evening Primrose (Œnothera) are correlated with observable alterations in the organisation of the fertilised egg-cell, especially as regards the *chromosomes*. In his "Mechanism of Mendelian Heredity" (1915) T. H. Morgan shows, for instance, that a particular unit-character in the fruit-fly (*Drosophila*) is almost certainly correlated with a change in a definitely localised area of a single chronosome.

§ 6. *Practical Importance of Mendel's Discovery*

As Mendel's discovery is extended it is bound to have a great influence on the breeding of animals and the cultivation of plants. Wherever it is applicable it will afford a solid basis for action, enabling the breeder to reach his desired result more surely, more rapidly, and more economically. The case we have mentioned of the varieties of wheat susceptible and immune to "rust" is in itself very suggestive.

A case like that of the Andalusian fowls shows how immediate may be the practical utility of Mendelism. The pairing of blue Andalusians yields only six blues to the dozen; the crossing of a black and a white yields twelve blues to the dozen.

The impossibility of fixing the blue Andalusian characters into a stable race is simply due to the fact that the blue Andalusians are hybrids, and the same is probably true of cases like the sugar-beet, where selection seems to have ceased to produce further improvement.

The breeder who wishes to get a stable and pure strain rapidly, has obviously a clue in the behaviour of the extracted recessives and the extracted dominants of the F^2 generation. There are many similar practical applications of Mendelian results.

Inbreeding.—Breeders who have with carefulness evolved a fine herd are often very loath to introduce fresh blood, even when they suspect that they are approaching the limits of safe inbreeding. But *if* Mendelism applies to the organisms bred, then it does not seem as if the introduction of fresh blood need affect the purity of the stock. A cross is effected to secure

reinvigoration; when the results of the cross are inbred, forms like the original parent will reappear.

Old-established form. "Fresh blood."

A **B**

If A be dominant, A(B); or B(A), if B be dominant.

× ×

A A

n A + *n* A(B) *n* A + *n* B(A)

Or if A(B) be inbred the result will be *n* A + 2 *n* A(B) + *n* B.

Or if B(A) be inbred the result will be *n* A + 2 *n* B(A) + *n* B.

There is obviously no *theoretical* danger of losing A.

No one can, of course, at present say that these "simple equations" will apply to the introduction of fresh blood into a herd of cattle, but the time has come for more daring experiment on Mendelian lines. It might obviously happen that the "fresh blood" (B) introduced was quite incompatible with the pure-bred (A), and the progeny was an undesirable freak. But do not such casualties happen under the present instinctive or empirical régime followed by most breeders?

§ 7. *Other Experiments on Heredity*

Our survey of cases must be supplemented by reference to the works of Bateson, T. H. Morgan, Punnett, De Vries, and others; but we have said enough to show,—(1) that Mendelian phenomena are well illustrated in certain cases—*e.g.* peas, mice, rabbits, poultry, snails; (2) that in other cases, while there are clear Mendelian phenomena according to some observers, discrepant results have been reached by others—*e.g.* silk-moths; (3) that in other cases, while there are hints of Mendelian phenomena, the results cannot be readily interpreted in conformity with Mendelism—*e.g.* pigeons.

Of great interest are Johannsen's experiments with pure lines of beans, which go to show that small quantitative fluctuations are in this case unimportant, the real evolutionary steps being attained by brusque variations, corresponding to Darwin's sports and De Vries's mutations. Selection continued generation after

generation in a particular pure line may fail to secure any result, *e.g.* in the average size of the seed. Thus a *ne plus ultra* may be attained by a line. Similarly, as regards certain characters in guinea-pigs, Castle has repeatedly attempted without success to bring about a change by selecting within an inbred race. "Thus a very dark form of Himalayan albino, after a certain amount of improvement by selection, could not be further darkened to any appreciable extent" (*Journ. Washington Acad. Sci.*, vii., 1917, pp. 368–387). But what must be avoided is generalising from particular sets of facts.

Thus it is certain that in many cases the principle of the pure line does not apply. Certain characters of guinea-pigs, rabbits, and rats have been found to respond readily to selection in a particular direction. Moreover, even Johannsen has shown that mutations may occur within pure lines, and these may afford material for selection.

Different sets of data suggest different conclusions, and these need not be contradictory. "A study of albinism alone," Castle says, "would lead one to believe in the fixity and constancy of Mendelian genes, and the impossibility of modifying them by selection. A study of white-spotting leaves one with the unshakable conviction that this form of gene is plastic and yields readily to selection. Where only genes of the former sort are involved, the principle of the pure line is applicable; where genes of the latter sort are involved, it is not applicable." It is inadvisable to stereotype conclusions amid the rapid progress of a young science.

Castle inclines to the view that in the smaller mammals, which he has particularly studied, very few characters can be safely referred to the agency of perfectly stable hereditary factors or genes. Very important is his conclusion that, "aside from colour, there are very few valued economic characters in our domestic animals which are not inherited after the manner of blends" (see *Journ. Washington Acad. Sci.*, vii., 1917).

As was to be expected, the discoveries of the Mendelian experimenters have raised problems in solving others, and various elaborations have been found necessary in order to

bring or keep certain phenomena within the scope of Mendelian interpretation. It may be that some of the subtleties of formulation are necessary and transitional; it may be that some of the difficulties are due to over-stretching the Mendelian concepts.

One of the active experimenters has given expression to this. "From the simple conditions discovered by Mendel there has arisen through the work of the last decade an array of observations tending to show that the Mendelian phenomenon is not in many instances as distinct and simple as one might wish, and at present diverse kinds of variability in the behaviour of characters are described and attributed, in some instances, to several different kinds of latency, to gametic coupling, to variable potency, to variable dominance, and so on. The situation essentially is this, that as investigation has progressed it has been discovered that not one, but a host of determining factors (I use the word factor as meaning something that makes possible a given result, with no idea expressed or implied as to the nature of this factor) are operative in the production of alternative inheritance; and in the attempt to preserve the letter of the law of Mendelian theory of unit-characters with segregation in gametogenesis, a host of hypotheses have been developed in order to save the original theory" (W. L. Tower, 1910).

Tower's Experiments.—Great interest attaches to the experiments of Prof. W. L. Tower (1910) on crossing species of potato-beetle (*Leptinotarsa*). In these experiments the chief variables were the conditions surrounding and incident upon the germ-cells at the time of fertilisation, and it was found that changes in the external conditions (temperature, humidity, etc.) are associated with changes in the alternative (Mendelian) inheritance. He succeeded "in creating a series of behaviours in which the same characters are dominant to the complete exclusion of others; dominant to a lesser degree, or in which there is a complete blend between the two in the F^1 generation, or the appearance of both parental types in F^1 and both breed true."

The question of dominance, according to these experiments, is not entirely dependent on the constitution of the germ-cells, it is partly dependent on the external conditions operative on the germ-cells at the time. In short, conditions external

to a cross are important factors in determining the results thereof in somatic expression.

Tower's general conception of the attributes of the organism appears to us to have a wholesome breadth and elasticity such as the present state of knowledge demands. He recognises the following facts as regards organic constitution:

"1. That there is in organisms a form basis, relatively unalterable as regards symmetry, pattern and arrangement of parts.

"2. That there are in organisms an array of attributes capable of variation, but blending in heredity, forming blends and intermediates.

"3. That there are in organisms an array of attributes which can exist only in a definite state of stability—they are either there or not there.

"4. That there are in organisms characters that by crossing can be replaced by other more or less similar but different characters."

Johannsen's Experiments on Pure Lines.—Experiments by Nilsson and others at Svalöf in Sweden have shown that the progeny of an isolated particularly good ear of barley may all exhibit the parental characters, and that their progeny in turn breed true. If a single plant exhibits a desired result it is shortest and surest to work from it alone, without going on for years selecting also the nearest approximations. We owe to the Danish botanist Professor Johannsen an elaboration of this idea in a series of very important experiments, carried out with unsurpassed patience and precision. He calls all the descendants of a single individual in a self-fertilising race a "pure line." An apparently homogeneous race or "population" is a congeries of pure lines. Given an isolated pure line, the cultivator can get no more out of it; there are plus and minus "fluctuations," but even with selection there is always a return to the average. Similarly, in a population, which is made up of a congeries of pure lines, selection cannot do more than

isolate the best pure lines, it cannot get beyond the extremes which the included pure lines illustrate.

One of Johannsen's main results was to show that a pure line is very constant from generation to generation. There are many individual differences, but these do not tend to be reproduced in the offspring. They appear to be *modifications* due to peculiarities in the "nurture" of individuals. There do not appear to be the numerous germinal variations which are so often postulated. If a big hereditary change occurs, it comes

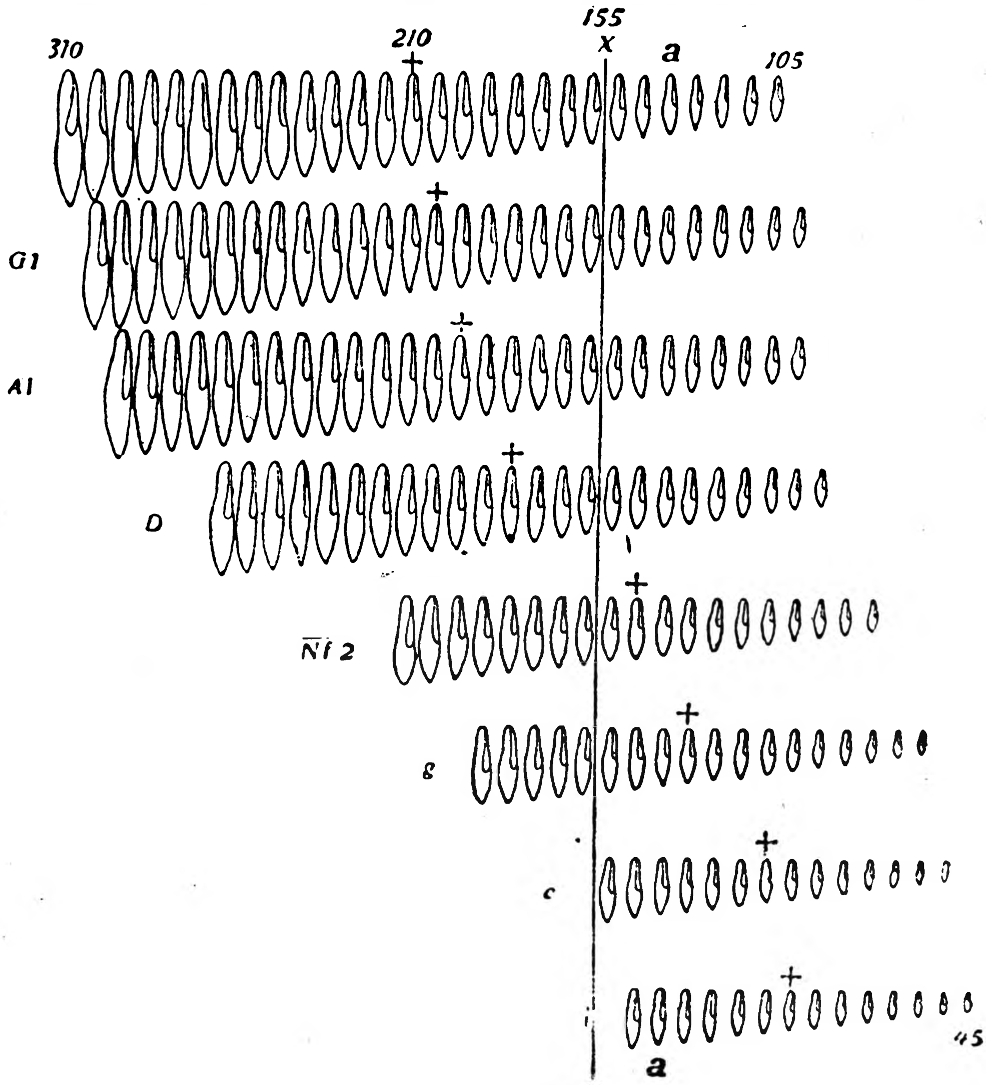

FIG. 40*a*.—Pure Lines in Paramœcium. (From Jennings.)

about by a "mutation" in the pure line, not by selection among the individual differences.

Jennings has illustrated the significance of "pure lines" in reference to the slipper-animalcule (*Paramœcium*). The figure shows a population made up of eight pure lines, each of which is marked by a certain range of size. The line *x—x* indicates the mean of the populate; the crosses indicate the means of the several lines. If a giant be isolated from the first line, its progeny, kept in the same conditions, keep up the characters of that line. The large-sized stock thus arising can hardly be called the result of selection from the population in question; it is the result of the isolation of an individual of a particular pure line. And the other point is, that no amount of selection will get anything out of the isolation beyond the limits of the pure line from which it came.

The conclusion that experiments on "pure lines" suggest is one towards which many lines of modern experimentation point, namely that in certain sets of cases the variations that count are mutations, not fluctuations. By a germinal stride a most excellent ear of wheat is formed; there is more to be got out of that single ear than out of years of selection of smaller fluctuations. The fact that, although plus and minus fluctuations occur in the pure line, selection can make nothing more of them, seems to show that these small fluctuations are often not transmitted. It is probable indeed that many of them are not *germinal variations* at all, but *acquired modifications* due to diversities of nurture. There is a question, however, which must not be left out of account, namely, whether the individual new departures, which are often far from abrupt or startlingly discontinuous, may not be the outcrop of the long-continued selection of forms showing small fluctuations. This is, indeed, suggested by the conclusion of some investigators, though not of De Vries, that a mutation is a stride in the same direction as that of the majority of the fluc-

tuations. And it may be that small fluctuations, not in themselves demonstrably heritable, may, in the course of generations of consistent selection, be summed up in heritable mutations. This would not exclude another possibility that mutations are due to deeply saturating environmental influence.

Hybridisation in General.—It is not desirable to attempt to draw any definite line between the various kinds of crossings—which may all be arranged on an inclined plane—for they differ simply in the degree of difference between the two parents. We may conveniently use the word "hybridisation" (cross-breeding, outbreeding, exogamy) whenever there is a marked difference between the two parents. The cases may be arranged on an inclined plane.

.. .. Different genera.
.. .. Different species.
.. .. Different subspecies.
.. .. Different breeds.
.. .. Mutants.
.. .. Variants.
.. .. Apparently identical forms.
.. .. Self-fertilisation (autogamy).
.. .. Parthenogenesis.

Examples.—Individuals belonging to different *genera—e.g.* domestic fowl and pheasant, sea-urchins, different genera of orchids.

Individuals belonging to different *species—e.g.* capercaillie and black grouse, carrion crow and hooded crow, different species of *Saturnia*, different species of *Medicago*.

Individuals belonging to different subspecies—*e.g.* maize.

Individuals belonging to different breeds—*e.g.* poultry, Short-horn and Aberdeenshire Angus cattle, Clydesdale and Shire horses, silkmoths.

Individuals belonging to different "varieties" which have not risen to the stability of "breeds"—*e.g.* wheat susceptible and immune to rust.

Hybridisation of Distinct Species.—The conception of species

is confessedly quite relative—it is *a term of convenience* when we wish to include under one title all the members of a group of individuals who resemble one another in certain characteristics. A species is often simply a segment of a curve of closely related forms. It is a statistical conception, and as there is no absolute constancy in specific characters, as one species melts into another, with which it is connected by intermediate varieties, by frequent or casual variations, we have to confess that it is a human device, the validity of which varies greatly according to our knowledge or ignorance of the forms in question. A specific name is sometimes, when we are very ignorant, as unmeaning as the name of a constellation in the starry heavens. But it is equally convenient.

At the same time, since science is systematised common sense, it is usually admitted—oftener, perhaps, as a pious opinion, than as a practice—that the characters on account of which a naturalist gives a specific name to a group of similar individuals *should be more marked than those which distinguish the members of any one family, should show a relative constancy from generation to generation, and should be associated with reproductive peculiarities which tend to restrict the range of mutual fertility to the members of the proposed species* (see the author's *Outlines of Zoology,* 5th ed., 1910, pp. 14-16).

The popular impression that crosses between "distinct species" are rare is erroneous; for, apart from the familiar mules, fertile pairing is known between lion and tiger, dog and jackal, wild and domestic cat, brown bear and polar bear, American bison and European wild ox, horse and zebra, hare and rabbit, duck and goose, canary and finch, thrush and blackbird, capercaillie and blackcock, carrion crow and hooded crow, pheasant and fowl, and the list soon becomes very long if we include backboneless animals and plants (see *Evolution of Sex,* revised ed., 1901, p. 163).

The popular impression that fertile crosses between "distinct

species" result invariably in sterile offspring is also erroneous; for the hybrids of American bison and European wild ox, of Indian humped cattle and domesticated ox, of common goose and Chinese goose, of common duck and pintail duck, of different kinds of pheasants, and many more are certainly fertile.

At the same time, it seems safe to say that the likelihood of successful crossing and of the fertility of the hybrid offspring is in inverse proportion to the distinctness of the species crossed.

It seems also safe to say that the characters of species-hybrids do not conform to any general formula. They may be a blend of the parental characters, they may be exclusive or particulate, they may be reversionary—*i.e.* allowing expression of long-latent ancestral characters—or they may be novel and peculiar.

On the whole, the crossing of distinct species, while it may be interesting physiologically, does not seem to have much interest for the evolutionist. It does now and then occur in nature, but it seems to be a mere by-play of little phylogenetic importance—unless perhaps in very early days, of which we know nothing.

Diverse Results of Hybridising.—An inheritance is such a complex integrate of items that no one can hope to predict the result of mingling two more or less distinct inheritances. We have two organisms, A and B, which can be crossed and produce offspring: but, before the germ-cells of A and B are ready for union, they have undergone a process of maturation which may definitely affect the burden of hereditary qualities of which each germ-cell is the vehicle; by the process of amphimixis or fertilisation a new integrate or zygote is formed—the fertilised egg-cell—and in this integration the inheritance may be affected by permutations and combinations, mutual adjustments and new states of equilibrium, victories and defeats of particular items, of all which we have no actual knowledge. In the process of development, if there are several different sets of primary constituents representative of a future structure—an hypothesis from which we can see no escape—then the result

may in part depend on the struggles and interactions of these in the course of development; for, as we have often said, it does not follow that everything represented in the inheritance finds expression in development. Finally, it must be remembered that the process of development implies interaction between the inheritance and an appropriate environment, and that since this appropriate environment is variable (within limits of the embryo's viability) the result may again be *modified* by minor peculiarities of nurture. It is, therefore, plain that prediction as to *individual* results of crossing is out of the question.

The Mendelian theory has thrown light on the variability which has often been remarked when crosses have been effected. Cross-breds are produced and inbred, and new forms appear in their progeny. The Mendelians contend, in Mr. Bateson's words, that "in all the cases which have been properly examined these *new* forms are created by simple re-combination of characters brought in by the original parents."

SUMMARY.—There are several well-known results of hybridisation:

1. The hybrids may be an intermediate blend of the parental characters, as in mulattos, finch and canary, carrion crow and hooded crow, and in many plants.—

$$A \times B \text{ yields } \frac{AB}{2}$$

2. The hybrids may show a particulate juxtaposition without a blend of the parental characters, as in piebald animals, or in the cross between male Lady Amherst pheasant and female golden pheasant,—

$$A \times B \text{ yields } \frac{A + B}{2}$$

3. The hybrids may resemble an ancestral form, whose characters have not been recently patent, as in many crossings of pigeons, red-eyed albino house-mouse and

Japanese waltzing mouse (with progeny like wild mouse), white Angora rabbit and Belgian hare rabbit (with progeny like wild rabbit),—

A × B yields *r* (AB)

4. The hybrids may be quite different from either parent "with a character of their own"—*e.g.* Andalusian fowl,—

A × B yields C

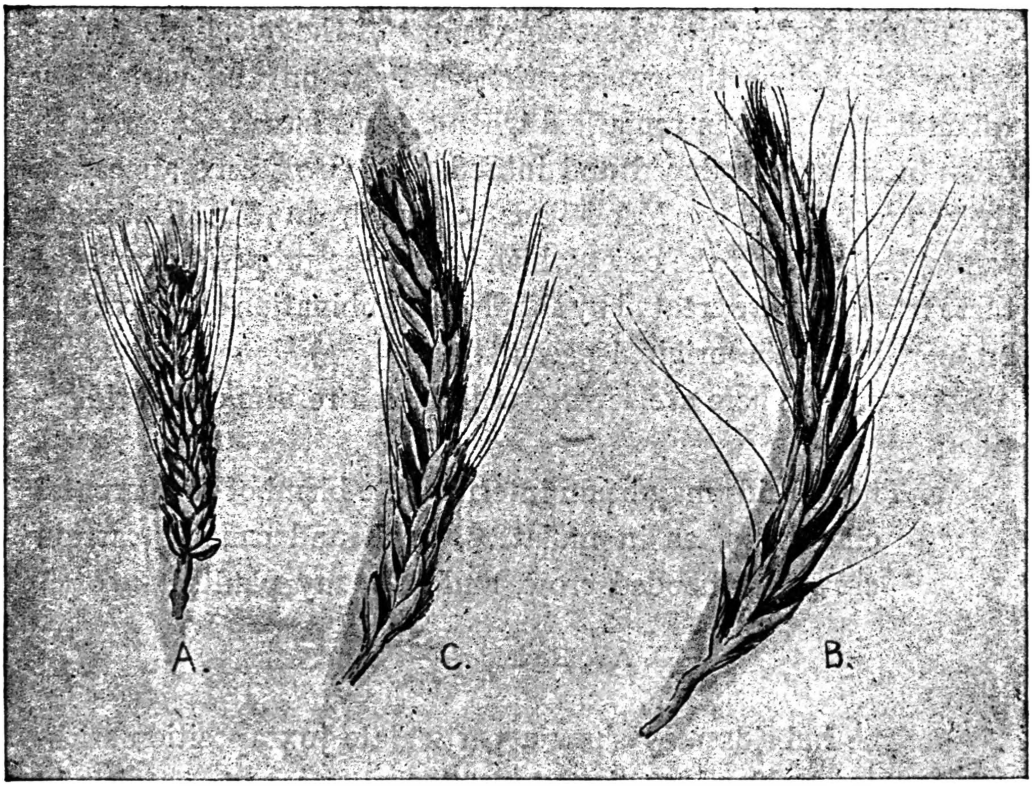

FIG. 41.—Varieties of Wheat. (After R. H. Biffen.)

A, Rivet; B, Polish; C, The hybrid Rivet × Polish, intermediate in laxness and glume length between its parents.

5. The hybrids may exhibit the (dominant) characters of one parent, the (recessive) characters of the other parent remaining latent; this is the first step in Mendelian inheritance,—

A × B yields A(B)

It has been stated in some cases,—(*a*) that the hybrid shows more of the character of that parent which is phyletically older or more securely established—see *e.g.* some of the results of Standfuss; (*b*) that the hybrid shows more of the character of that parent whose gametes were relatively more mature at the time of fertilisation—*e.g.* some of the results of Vernon. Other generalisations have been ventured, but all require to be revised in the light of what we now know of Mendelian phenomena.

It remains to be seen how far the known cases of blended, exclusive, and particulate inheritance are interpretable as forms of Mendelian or alternative inheritance, and there are many who suspect that the result will be the great extension of the Mendelian interpretation. Until we have wider knowledge of unit characters and of their alternative inheritance we must retain the descriptive terms—blended, exclusive, and particulate. In many cases where there is a pairing of closely similar organisms, the most striking fact is the uniformity of the inheritance—which we might describe as *continuous*.

It may seem strange, at first sight, that there can be any question of bringing a "blend" within the Mendelian category. But where we have to deal with a multiplicity of independent characters, some dominant on the paternal side, some on the maternal side, the *impression* that there is blending in the offspring may readily arise, and still more when we come to the mixtures in the next (F^2) generation.

What is called particulate inheritance may be due to the alternative inheritance of the elements of a patchwork of characteristics, which, as Galton said, "are usually transmitted in aggregates, considerable groups being derived from the same progenitor." He went on to say: "Skin-colour is a good example of what I call blended inheritance. It need be none the less 'particulate' in its origin, but the result may be regarded as a fine mosaic too minute for its elements to be

distinguished in a general view" (*Natural Inheritance*, 1889, chap. ii.).

Sometimes, as in mules, the hybrid offspring are sterile. This may show itself (1) in atrophy of the reproductive organs, (2) in abnormalities in the reproductive ducts; or (3) in more obscure conditions in regard to which we can only shroud our ignorance with the words, "constitutional incapacity."

§ 8. *Consanguinity*

Consanguinity.—In many peoples—Jewish and Mohammedan, Indian and Roman—laws against the marriage of near kin go back to remote antiquity, but it seems probable that the basis of these was social rather than biological. In other peoples—Persian, Phœnician, Arab, and even Greek—consanguineous marriages were permitted and sometimes encouraged. The idea that the marriage of near kin is a cause of degeneracy seems to be relatively modern, and is probably based in large measure on the observed degeneracy in closely intermarried noble families. In certain closely inbred communities, moreover, a large percentage of deaf-mutes and weak-minded has been often observed. But it is not difficult to find counter-instances—*e.g.* in the Norfolk Islanders and in the people of Batz on the lower Loire—where close inbreeding has *not* been followed by ill-effects. Mr. George H. Darwin has made out a strong case in support of the position that consanguineous marriages are not in themselves causes of degeneration or of diminished fertility.

Biologically it seems certain that close inbreeding can go far without any ill effects, but further in some types than others. Many plants, such as garden-peas, wheat, and oats are habitually self-fertilising; the same is true of a few of the hermaphrodite animals, *e.g.* the parasitic flukes and tape-worms. But these are cases which have become adapted to this sort of (auto-

gamous) reproduction—the extreme of in-breeding. The practically important inquiry is in regard to the limits of profitable in-breeding among types which are normally cross-breeders or exogamous.

Darwin's Conclusions.—Charles Darwin devoted much attention to the question of inbreeding (see especially his *Animals and Plants under Domestication*), and his conclusions were: (1) "The consequences of close interbreeding carried on for too long a time are, as is generally believed, loss of size, constitutional vigour, and fertility, sometimes accompanied by a tendency to malformation"; (2) "The evil effects from close interbreeding are difficult to detect, for they accumulate slowly and differ much in degree in different species, whilst the good effects which almost invariably follow a cross are from the first manifest"; (3) "It should however be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigour."

Experiments.—Weismann inbred mice for twenty-nine generations, and his assistant Von Guaita continued the inbreeding for seven more generations. The general result was a notable reduction of fertility—about 30%.

Ritzema-Bos inbred rats for thirty generations; for the first four years (twenty generations) there was almost no reduction of fertility, but in the following generations there was very marked decrease of fertility, increase of mortality, and decrease of size. But there was no disease or abnormality, such as other experimenters—*e.g.* Crampe—have observed. It goes without saying that if there is a diseased stock, or rather a stock with an hereditary predisposition to disease to start with, then the evil results of inbreeding will soon be evident. But the point is, what will happen if the stock be healthy?

Extensive experiments by Castle and others on the inbreeding of the pomace-fly, *Drosophila ampelophila*, led to the general

result that "inbreeding probably reduces very slightly the productiveness of *Drosophila*, but the productiveness may be fully maintained under constant inbreeding (brother and sister) if selection be made from the more productive families."

Castle (1911) also reports that a polydactylous race of guinea-pigs all descended from one individual remained exceedingly vigorous for ten years and then showed no hint of diminishing fertility.

While it seems certain that prolonged and close inbreeding may afford opportunity for an inherent taint to show itself, to spread, and to accumulate, it is not the consanguinity that is to blame for the taint. The same consequences would probably result if matings took place among *unrelated* organisms with the same kind of taint.

In regard to cousin marriages in mankind the family history should be carefully scrutinised. The likelihood of unhealthy offspring will be very great if there are the same hereditary taints in the lineage of both parents. If there is a well-defined family predisposition to certain diseases, the fact that the cousins are somatically healthy does not warrant their becoming parents. If two somatically healthy cousins belonging to a tainted family have what is called a single or simplex dose of the taint, the probability is that on the average one quarter of the children would be unhealthy. On the other hand, if the family history is good on both sides, there is no biological reason why two healthy cousins, who fall in love with one another, should not marry and have children.

Some variations are from the first so stable that their persistence is certain without any precautions of inbreeding. But, in other cases, it appears to be the experience of breeders that a period of inbreeding, with elimination of any " weeds " that may crop up, serves to fix characters, developing " prepotency " in regard to the desired qualities. Crossing may then be resorted

to without any fear of the excellence being lost, and with the expectation of an increased stimulus to vigour.

It seems well established that some stable and important breeds of cattle—*e.g.*, polled Angus—have arisen under conditions involving in the early stages extremely close inbreeding, and it is well known in horse-breeding that very valuable results have been reached by using the same stallion repeatedly on successive generations.

Thus, if we take the pedigree of the short-horn bull " Courtier," calved January 6th, 1896, owned by the Iowa Agricultural College, we find from the tabulation given by Mr. R. W. Barclay that " Champion of England " (17526) appears in the pedigree over twenty-five times, and " on both sides of the house." We find another famous bull, " Roan Gauntlet " (45276), functioning over and over again in the lineage. Let us take, for instance, the pedigree of the paternal grandfather of " Courtier " (see p. 390).

The whole subject has been recently illumined by East and Jones in their fine work on *Inbreeding and Outbreeding* (1919). It is shown that inbreeding of good stock, accompanied by judicious elimination of " wasters," *fixes* desirable characters, and leads to a stable and uniform herd. Yet it is sometimes associated with reduction of vigour, resisting power, fecundity, and even size. This is not because of the consanguinity as such, but because the inbreeding automatically brings into expression a number of undesirable " recessive " characters, hidden in conditions of exogamy by their " dominant " counterparts. But this exposure of undesirable features may be utilised by the breeder for the useful purgation of the herd. Needless to say, when the same undesirable features occur on both sides of the house, inbreeding tends to diffuse and exaggerate them. The value of exogamy or outbreeding is two-fold. It brings about a greater variety of raw material on which selective agencies can work. It also promotes " hybrid vigour " by the pooling of diverse hereditary resources of good quality. The crossing makes it more likely that a minus on one side may be made good by a plus on the other, or that desirable dominants may strengthen one another's hands.

- Courtier
  - Prince Bishop
    - Dunblane
      - Roan Gauntlet
        - Royal Duke of Gloster
          - Grand Duke of Gloster
            - Champion of England
            - Duchess of Gloster 9th
          - Mimulus
            - Champion of England
            - Mistletoe
        - Princess Royal
          - Champion of England
            - Lancaster Comet
            - Virtue
          - Carmine
            - The Czar
            - Cressida
      - Duchess of Gloster 21st
        - Barmpton Prince
          - Viceroy
            - Champion of England
            - Violet's Forth
          - Butterfly's Delight
            - Allan
            - Butterfly's Joy
        - Duchess of Gloster 13th
          - Grand Duke of Gloster
            - Champion of England
            - Duchess of Gloster 9th
          - Duchess of Gloster 12th
            - Champion of England
            - Duchess of Gloster 7th
    - Duchess of Gloster 24th
  - Sweet Charity 4th. In the dam's lineage we find, just as above, Barmpton Prince, Princess Royal, Roan Gauntlet, Royal Duke of Gloster, Viceroy, Butterfly's Delight, and Champion of England.

CHAPTER XI

HISTORY OF THEORIES OF HEREDITY AND INHERITANCE

"Like leaves on trees the race of man is found,
Now green in youth, now withering on the ground;
Another race the following spring supplies,
They fall successive and successive rise."

ILIAD (*Pope's Translation*).

[The same may be said of the succession of theories of heredity, but, in both cases, there is a persistent living tree, to whose growth all the leaves contribute.]

§ 1. *What is required of Theories of Heredity and Inheritance.*
§ 2. *The Old Theories of Heredity.*
§ 3. *Theories of Pangenesis.*
§ 4. *Theory of Genetic or Germinal Continuity.*

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§ 1. *What is required of Theories of Heredity and Inheritance*

THE main object of a theory of heredity is to express in as simple terms as possible the nature of the genetic relation which binds generations together, and to interpret the facts of inheritance in terms of this relation.

The Uniqueness of the Germ-Cells.—The first and chief problem is to account for the material basis of heredity—*i.e.* in all ordinary cases, for the germ-cells. What is their origin and history ? what relation have they to the parental body which bears them, from which they are liberated ? what relation have they to the germ-cells of the body into which they develop ? Or, more generally, in what way are they peculiar ? how do they

differ from ordinary cells? to what do they owe their unique reproductive power? In short, what enables them to develop into organisms like the parent-organisms? To these questions it is possible to give a satisfactory answer.

The Architecture of Inheritance.—The second problem is of a different nature, and much more difficult. In some way, every one must admit, the germ-cells or gametes are potential organisms. Without any aid except that afforded by an appropriate environment, they can develop into complete organisms. In some way, the organism, the inheritance, lies *in posse* in the germ-cells. Can we form any image of this? Can we construct any hypothetical scheme of the manner in which the inheritance is organised within the germ-cells? Chemists frame hypothetical conceptions regarding the structure of chemical molecules, and judge of the validity of these by their usefulness in formulating the changes which the molecules undergo in certain conditions; physicists make similar mental pictures—imaginary models—of the constitution of atoms and so on. Can biologists do the same in regard to the material basis of inheritance?

This is the fundamental problem of inheritance, and it can only be approached indirectly. The organisation can never be seen or verified; all the complexities in germ-cells which microscopic analysis reveals are not more than the rough outlines of the real edifice—the edifice which the scientific imagination must build. But the speculative construction is not left to irresponsible fancy; it must be such that it corresponds to and enables us to formulate the visible and measurable facts of inheritance, and the processes of development. It must be harmonious with the large generalisations of inheritance, such as Mendel's law or Galton's law; it must also be harmonious with every peculiar phenomenon, such as resemblance to a remote ancestor.

Theory of Development.—A careful study of the history

of the germ-cells enables us to form *a general theory of heredity* enables us to understand how the germ-cells have their peculiar reproducing power.

A consideration of the facts of inheritance, both general and special, enables us to form *a general theory of inheritance*—*i.e.* a speculative thought-model of what the architecture of the germinal material may or must be.

But it is also necessary to try to form some picture of what occurs during development. The inheritance is in some way expressed, the potentialities are realised, the legacy is cashed—can we form any image of what occurs? As before, our image may not be actually what occurs, but it must not contradict anything that occurs, and, more positively, it must help us to formulate what occurs. This is the business of *the theory of development*.

Other Theories are involved.—The result of development is always an organism more or less like the parent, but the completeness of hereditary resemblance is usually affected by the occurrence of variations, sometimes minute and quantitative, sometimes large and qualitative. It is evident, therefore, that theories of heredity, inheritance, and development must be supplemented by *a theory of variation.*

Nor is it possible to abstract the theory of heredity and inheritance from the theory of growth, reproduction, and sex; from the theory of environmental and functional influences which we sum up in the term "nurture"; from the theory of the correlation of psychical and corporeal life; and from the general theory of organic evolution in which all biological theories are combined.

But while we recognise that abstraction of particular problems is merely a device to facilitate clear thinking, and by no means without the counterbalancing dangers which all abstraction involves, we propose in this chapter to restrict our attention to the theories of heredity and inheritance, and to give a general historical retrospect.

It cannot be said that this historical retrospect leads us to any complete and satisfactory interpretation of all the puzzling facts which are covered by the word "heredity," but it will indicate some of the main attempts which have been made, and which of these are most promising. We must still recognise the justice of Herbert Spencer's words:

"A positive explanation of heredity is not to be expected in the present state of biology. We can look for nothing beyond a simplification of the problem, and a reduction of it to the same category with certain other problems which also admit of hypothetical solution only. If an hypothesis which certain other wide-spread phenomena have already thrust upon us can be shown to render the phenomena of heredity more intelligible than they at present seem, we shall have reason to entertain it." *

§ 2. *The Old Theories of Heredity*

There have been many attempts at theories of heredity and inheritance, but it is not profitable to say much about the earlier ones, most of which were theological or metaphysical rather than scientific. It will be seen, however, that shrewd enough ideas are sometimes hidden in the old theories, whose phraseology no longer appeals to the scientific mind.

(*a*) **Theological Theories.**—In olden times the idea was prevalent that the germ of a new human life was at conception possessed by a spirit, which thereafter became responsible for development. As it is not so very long ago (1760 or later) that even digestion was explained as the work of a spirit, it need not surprise us that development was relegated to a similar unverifiable efficiency. Sometimes the spirit was, so to speak, of second-hand origin, having previously belonged to some ancestor or to some animal. The idea of successive reincarnations has had many expressions in the West as well as in the East.

* Herbert Spencer, *Principles of Biology*, vol. i. (1st ed. 1863).

So far as the idea persists in the minds of civilised men, it is so much purified and sublimed that, if it does not appeal to the student of science as what he would call true, it is at least such that he cannot wisely call it false. For we believe in mosaic or ancestral inheritance, and though we know that this has a definite material basis, we have no warrant for denying that this has also its metakinetic or spiritual aspect. In any case, there is more than a metaphor in such phrases as "the hand of the past," or "the beast in the man."

(*b*) **"Metaphysical" Theories.**—For a time, especially in the latter half of the eighteenth century, it was the custom to appeal to *vires formativæ*, "hereditary tendencies," and "principles of heredity," by aid of which the germ was supposed to grow into the likeness of its parents. It was in part the old story of explaining the working of the clock by "the principle of horologity," and in part a pedantic way of saying "We don't know."

Nor need we sneer at our predecessors in this respect, for the tendency to resort to verbal explanations is hardly to be driven from even the scientific mind except by severe intellectual asceticism. And in so far as it expresses a respectful ignorance, a consciousness of the complexity of the problem, an awareness that we have still to use x (the power of life) in our biological equations, such "metaphysical" mist is perhaps preferable to the frost of a materialism which blasts the buds of wonder and gives an illusory clearness to the vision.

Although William Harvey (1578–1657), working "in the harness of Aristotle," maintained that "all animals are in some sort produced from eggs," he at the same time believed in spontaneous generation as firmly as his master did. Although he maintained that the living creature begins in an apparently simple *primordium* in which "no part of the future offspring exists *de facto*, but all parts inhere *in potentia*," he was quite unable to suggest or give any scientific account of the *primordium* and its powers of development. He was forced to fall

back on a metaphysical conception of inheritance and development. "Not only is there a soul or vital principle present in the vegetative part, but even before this there is inherent mind, foresight, and understanding, which, from the very commencement to the being and perfect formation of the chick, dispose and order and take up all things requisite, moulding them in the new being, with consummate art, into the form and likeness of its parents."

(*c*) **"Preformationist" Theories.**—During the seventeenth and eighteenth centuries, and even within the limits of the nineteenth, a theory of inheritance and development prevailed, according to which the germ (either the ovum or the sperm), contained a miniature organism, pre-formed though invisible, which only required to be unfolded ("evolved") in order to become the future animal.

Moreover, the egg of a fowl contained not only a micro-organism or miniature model of the chick, but likewise, in increasing minuteness, similar models of future generations. Thus the rash theorists pointed out that Mother Eve must have included 1,543,657—or, according to another computation, 200,000 million—homunculi; and, what was still more rash, they *figured* the miniature homunculus which lay within the sperm. The "ovists," who held that the ovum contained the miniature, did battle with the "animalculists," who supported the claims of the sperm; but both schools agreed in the general idea, that microcosm lay within microcosm, germ within germ, like the leaves within a bud awaiting successive unfolding, or like an infinite juggler's-box, to the "evolution" of which there was no end.

A thoroughgoing representative of the preformationist school was Charles Bonnet (1720–93), who discovered the parthenogenesis of green-flies, and made many important observations on polyps and worms, but after the failure of his eyesight became more exclusively a speculative thinker. He pondered over

generation and development, and ended by almost denying them both. He assumed "as a fundamental principle, that nothing is generated, and that what we call generation is but the simple development of what pre-existed under an invisible form, and more or less different from that which becomes manifest to our senses." In the same way, the renowned physiologist, Albrecht von Haller, said "Es gibt kein Werden" ("There is no becoming"); and it became the fashion to declare that all development was an illusion—only an unfolding or *evolutio*. In contrast to Harvey's conclusion, "The first concrement of the future body grows, gradually divides, and is distinguished into parts; not all at once, but some produced after the others, each emerging in its order," Haller wrote, "No part of the body is made from another; all are created at once."

To the main conception of preformation and unfolding, two subsidiary hypotheses were added: (i) that of *emboîtement*, according to which the germ contains the preformation not of one organism only, but of successive generations; and (ii), that germs occurred scattered throughout the organism, capable of developing into buds, of replacing lost parts, and so forth—neither of them ideas to be laughed at, though their particular expression was necessarily erroneous.

The long-lived theory, variously termed the "preformation theory," the "theory of evolutio," the "mystical hypothesis," the theory of "emboîtement" or "Einschachtelung," or "die Skatulationstheorie," seemed to get its deathblow from Wolff's demonstration (1759) of "epigenesis," or the gradual development of obvious complexity from an apparently simple rudiment. We say "seemed," because the theory, as theories will, persisted long after the deathblow was given. Moreover, though Wolff demonstrated in the chick that gradual becoming which we call development, he had no way of accounting for the uniqueness of the germ-cells, and had to fall back on the postulate of a *vis corporis essentialis*.

Every one allows that the concrete expressions of the preformationist doctrine were crude and false. No microscope, however powerful, will show a miniature model of the future organism lying within either egg or sperm. But, as Huxley pointed out, the preformationists were obviously right in insisting that the future organism must indeed be materially implicit within the germ; and they were also right in supposing that the germ involved the rudiment not only of the organism into which it grew, but of the next generation as well. But the preformationists themselves had not and could not have any understanding of the two elements of truth which we can now read into their theories, and which are at present expressed in modern rehabilitations, (i) in the "evolutionist" conception of inheritance and development, and (ii) in the conception of germinal continuity. It is a mistake to think that either of these is in any direct way affiliated to the preformationist doctrine.

The preformationists stocked the germ with some sort of preformed model, quite unverifiable as they thought of it, and thus made development easy by reducing it to mere unfolding; but they could not account for the preformation.

Yet their antagonists were equally unsatisfactory, for as one of the most scholarly of embryologists, Prof. C. O. Whitman, has said, "Aristotle, Harvey, Wolff, and Blumenbach all traversed the same problem, and landed in the same pitfall. They all faced the question of preformation, and discovering no natural way by which the germ could come ready-made, they insisted that the germ must start anew every time and from the pit of material homogeneity, acquiring everything under the guidance of hyperphysical agencies, assisted by the accident of external conditions."

It was, indeed, a deadlock until concrete investigation disclosed the origin of the germ-cells with their heritage of organisation, until the actual nature of the genetic linkage between successive generations was disclosed.

§ 3. *Theories of Pangenesis*

Passing from theological, metaphysical, and mystical interpretations, we come to a whole series of theories, which are in varying degrees scientific, and may be fairly enough described by the general designation *pangenetic*. They all have this in common, that they seek to explain the uniqueness of the germ-cell by regarding it as a centre of contributions from different parts of the organism.

Early Forms.—We need not delay over the earlier and vaguer forms of this supposition. At such different epochs as are suggested by the names of Democritus and Hippocrates, Paracelsus and Maupertuis, incipient theories of pangenesis—prophecies of Darwin's—were suggested. Thus, Democritus maintained that the "seed" of animals was elaborated by contributions from all parts of the body, and that the constituent parts reproduced in development the organs and parts from which they had originated. Two millennia later, Buffon, of whose speculation Darwin appears at first to have been unaware, again conceived of the germs as mingled extracts from all parts of the body, or as collections of samples from the various organs. If such were indeed the case, Buffon and his predecessors saw no further difficulty, for each contributed sample produced in the development of the embryo a structure like its parental origin. Bonnet (1776) was another who suggested the possibility of molecules passing from the organs of the body to build up the germ.

Spencer's Theory of Physiological Units.—In 1861, the physiologist Brücke emphasised the usefulness of assuming the existence of biological units (*Elementarorganismen*) ranking between the molecule and the cell. In July, 1863, Herbert Spencer adopted a somewhat similar hypothesis of "physiological units," lower in degree than the visible cell-units, but more complex than the chemical molecules. As there is much in his

argument which seems useful to-day, we give a brief summary (see *Principles of Biology* (1st ed.), vol. i. p. 181 *et seq.*).

In the growth of an embryo from apparent simplicity to obvious complexity, in the regeneration of lost parts, in the regrowth of a whole by a part, the living substance arranges itself in definite form as some not-living substances do when crystallising out of a solution. In restating the fact, Spencer supposes that certain units composing the living substance possess "polarity," like the chemical units in crystallisation, meaning by "polarity" the unexplained power of definite arrangement. The units cannot be the chemical molecules of albumen and the like, for these do not show the particular kind of differentiation seen in growth; nor can the units be the cells, for the differentiation in question may be seen within the limits of a single cell.

"There seems no alternative but to suppose that the chemical units combine into units immensely more complex than themselves, complex as they are; and that in each organism, the physiological units produced by this further compounding of highly compound atoms have a more or less distinctive character. We must conclude that, in each case, some slight difference of composition in these units, leading to some slight difference in their mutual play of forces, produces a difference in the form which the aggregate of them assumes."

After the judicious sentences quoted on page 394, Spencer goes on to say: "The applicability of any method of interpretation to two different but allied classes of facts is evidence of its truth. The power which organisms display of reproducing lost parts, we saw to be inexplicable except on the assumption that the units of which any organism is built have an innate tendency to arrange themselves into the shape of that organism. We inferred that these units must be the possessors of special polarities, resulting from their special structures; and that by the mutual play of their polarities they are compelled to take the form of the species to which they belong." This is illustrated

by reference to the way in which pieces of a Begonia-leaf will reproduce the whole plant. "The assumption to which we seem driven by the *ensemble* of the evidence, is that sperm-cells and germ-cells [better, egg-cells] are essentially nothing more than vehicles, in which are contained small groups of the physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to." If the likeness of offspring to parents is thus determined, it becomes manifest, *a priori*, that besides the transmission of generic and specific peculiarities, there will be a transmission of those individual peculiarities which, arising without assignable causes, are classed as "spontaneous." So far, in our quotations, there is no distinct suggestion of the central idea of pangenesis nor of the transmissibility of modifications.

But Spencer goes on to say: "That changes of structure caused by changes of action must also be transmitted, however obscurely, from one generation to another, appears to be a deduction from first principles—or if not a specific deduction, still, a general implication. . . . The units and the aggregate must act and react on each other. The forces exercised by each unit on the aggregate, and by the aggregate on each unit, must ever tend towards a balance. If nothing prevents, the units will mould the aggregate into a form in equilibrium with their pre-existing polarities. If, contrariwise, the aggregate is made by incident actions to take a new form, its forces must tend to re-mould the units into harmony with this new form; and to say that the physiological units are in any degree so remoulded as to bring their polar forces towards equilibrium with the forces of the modified aggregate, is to say that when separated in the shape of reproductive centres, these units will tend to build themselves up into an aggregate modified in the same direction" (p. 256). That is to say, representative physiological units of the body congregate in vehicles which we call ova and spermatozoa, carrying with them, on their journey to form a new generation,

some definite and representative results of the modifications acquired by the parental body.

The physiological units may be compared to a band of travellers who found a settlement, who build houses and arrange many matters according to their "character," "tendency," "individuality," "polarity"—phrase it as one will. In course of time their constructed aggregate is modified by circumstances, by incident forces of war, want, weather, and the like, and the characters of the units are also modified; subsequently, some of them gather into "reproductive centres," which establish new aggregates, largely after the likeness of the first, and yet modified by the experiences endured.

On *a priori* grounds, this view seems not without plausibility, but Spencer's theory had to yield before the *fact* of germinal continuity.

Darwin's Theory of Pangenesis.—The best-known theory of this class is, of course, the "provisional hypothesis of pangenesis" suggested by Darwin in his *Variation of Animals and Plants under Domestication* (1868). The chief suggestions of this theory are well known to be as follows:

(1) Every cell of the body, not too highly differentiated, throws off characteristic gemmules;
(2) These multiply by fission, retaining their characteristics;
(3) They become specially concentrated in the reproductive elements in both sexes;
(4) In development the gemmules unite with others like themselves, and grow into cells like those from which they were originally given off, or they may remain latent during development even through several generations.

We do not know whether Mr. Darwin had seriously considered Mr. Herbert Spencer's hypothesis of "physiological units," but, as Prof. Ray Lankester points out, the hypotheses might be called complementary. "The persistence of the same material gemmule and the vast increase in the number of gemmules,

and consequently of material bulk, make a *material* theory difficult. Modified force-centres, becoming further modified in each generation, such as Mr. Spencer's physiological units, might be made to fit in with Mr. Darwin's hypothesis in other respects" (Ray Lankester, 1870, p. 32). "In fact, in place of the theory of emission from the constituent cells of an organism of material gemmules which circulate through the system and affect every living cell, and accumulate in sperm-cells and germ-cells, we may substitute the theory of transmission of force, the two theories standing to one another in the same relation as the emission and undulatory theories of light."

But we fear that this suggestion has only prophetic value, for we are not yet in biology in a position to utilise ideas of "modified force-centres" or "transmission of force." We must creep along with the slippery clue "metabolism" in our fingers!

One impression, however, we must emphasise—namely, that for the time Darwin's "*provisional* hypothesis of pangenesis" had all the merits of a warrantable scientific hypothesis, and had the marks of that insight of genius which the illustrious author was wont to deny in his humble conviction that "it's dogged as does it."

"Mr. Darwin wished to picture to himself, and to enable others to picture to themselves, a process which would account for (that is, hold together and explain) not merely the simpler facts of hereditary transmission, but those very curious though abundant cases in which a character is transmitted in a latent form, and at last reappears after many generations, such cases being known as 'atavism,' or 'reversion'; and again, those cases of latent transmission in which characteristics special to the male are transmitted to the male offspring through the female parent without being manifest in her; and yet again, the appearance at a particular period of life of characters inherited and remaining latent in the young organism." *

* E. Ray Lankester, 1890, p. 279; *Nature*, July 15th, 1876.

Jäger's Theory.—The next theory—Jäger's—is difficult to summarise, partly because of its technical character, partly because the author does not appear to be quite consistent in his statement of it at different times. The main points, under the present section, are as follows:

(1) Each organ and tissue contains, along with the molecules of its albumen, a specific "scent-stuff" (Duft- und Würzestoff).

(2) In hunger and similar experience the albumen liberates the "scent-stuff," which penetrates through the body as fatty acids, ethers, etc.

(3) These are specially attracted to the reproductive cells, which, when mature, are thus specialised by the reception of scent-stuff, and have in their protoplasm *vires formativæ* enough to reproduce a new organism like the parent.

It will be seen later on that this hypothesis of chemical pangenesis is not the most important contribution made by Jäger to the theory of heredity.

Galton's Modified Theory of Pangenesis.—From experiments on the transfusion of blood, Mr. Francis Galton was led to conclude that "the doctrine of pangenesis, pure and simple, is incorrect." But he did more than urge serious objections against Darwin's theory; he formulated one of his own, to which, with the exception of Prof. Herdman, subsequent investigators do not appear to have attached sufficient importance. The very important part of Galton's theory will be discussed in its proper place; it is not included in the series of pangenetic hypotheses. Galton is, in fact, one of the numerous biologists who have suggested the continuity of the germinal protoplasm. He is included at this stage, however, because he admitted as a subsidiary hypothesis a limited amount of pangenesis. To account for those cases which suggest that characters acquired by the individual parent are "faintly

heritable," Galton supposed that "each cell may throw off a few germs that find their way into the circulation, and have thereby a chance of occasionally finding their way to the sexual elements and of becoming naturalised among them." This part of his theory is obviously a cautious admission of limited pangenesis to account for a number of puzzling cases.

Brooks' Theory.—In 1883, in his valuable work entitled *The Law of Heredity*, Prof. W. K. Brooks gave full expression to a modification of Darwin's view of pangenesis. The main positions, which are here relevant, may be summarised as follows, almost in the author's words :

(1) The male and female cells are specialised in different directions ; their union gives variability.

(2) The ovum is a cell which has gradually acquired a complicated organisation, and which contains material particles of some kind to correspond to each of the hereditary characteristics of the species.

(3) The ovum reproducing its like, as other cells, gives rise not only to the divergent cells of the organism, but also to cells like itself.

(4) Each cell of the body has the power to throw off minute germs. When, through a change in its environment, its functions are disturbed, and its conditions of life become unfavourable, it throws off small particles which are the germs or gemmules of this particular cell.

(5) These germs may be carried to all parts of the body. They may penetrate to an ovarian ovum or to a bud, but the male cell has gradually acquired, as its especial and distinctive function, a peculiar power to gather and store up germs.

(6) In fertilisation each gemmule unites with that particle of the ovum which is destined to give rise in the offspring to the cell which corresponds to the one which produced the gemmule, or else it unites with a closely related

particle, destined to give rise to a closely related cell. Such a cell will be a hybrid, tending to vary.

(7) As the ovarian ova of the offspring share, by direct inheritance, all the properties of the fertilised ovum, the organisms to which they give rise will tend to vary in the same way.

(8) A cell which has thus varied will continue to throw off gemmules, and thus to transmit variability to the corresponding part in the bodies of successive generations of descendants until a favourable variation is seized upon by natural selection.

(9) As the ovum which produced this selected organism will transmit the same variation to its ovarian ova by direct inheritance, the characteristic will be established as specific, and transmitted henceforth without gemmules.

The above theory, being important, has been stated at some length. Apart from the suggestion of variation as due to sexual intermingling, with which Weismann has made us more familiar—apart, too, from the suggestion of germinal continuity, the credit of which Brooks shares—there are several important points to be emphasised in the modification proposed. It is in *unwonted and abnormal* conditions that the cells of the body throw off gemmules. The *male* elements are the special centres of their accumulation ; the female it is that keeps up the *general* resemblance between offspring and parent.

It is not proposed to enter into criticism of pangenetic theories. The best criticism is found in that abandonment of special hypotheses which more recent advances have rendered possible. It has often been urged that the hypothesis of pangenesis involves not one but many suppositions—that it is just as difficult to understand why a gemmule should reproduce a cell like its own origin as to understand the entire problem, and so on. Detailed criticism will be found in the works of Galton, Ribot, Brooks, Herdman, Plarre. and others. It is enough for us to emphasise

the comparative gratuitousness of any special theory whatever, a paradox which is explained in the succeeding section.

Apart from the fact that the pangenetic hypothesis is not in harmony with the results of experiments (*e.g.* on the transfusion of blood), or with what we know of the physiology of cells, it may be pointed out that the facts of inheritance are not such as might be expected if pangenesis were an actual occurrence. If it were, we should look for a frequent recurrence of, or for some specific hereditary influence from, exogenous morbid conditions, especially those associated with marked structural changes—for instance, injuries to the brain and spinal cord, cirrhosis of liver and kidney, cirrhotic induration of the lungs from dust inhalation. In fact, after a short series of generations the number of healthy subjects would be reduced to a minimum (Ziegler, 1886, p. 19).

§ 4. *Theory of Genetic or Germinal Continuity*

Owen.—As far back as 1849, Owen pointed out in his paper on parthenogenesis that in the developing germ it was possible to distinguish between cells which became much changed to form the body, and cells which remained little changed and formed the reproductive organs. This was probably the earliest distinct suggestion of the modern theory of germinal continuity.

Haeckel.—In 1866, in his classic *Generelle Morphologie*, Haeckel emphasised the simple and yet fundamental fact of the material continuity of offspring and parent. In an historical note upon the distinction between the "personal" and "germinal" parts of an organism, Rauber states that the distinction was proposed by Haeckel in 1874, and by himself in 1879.

Jäger.—Jäger stated the doctrine of germinal continuity very clearly and concisely at an early date: "Through a great series of generations the germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic

portion, out of which the individual is built up, and a phylogenetic portion which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as *the continuity of the germ protoplasm*. . . . Encapsuled in the ontogenetic material, the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters."

Brooks.—Brooks notes that, in papers published in 1876 and 1877, he had also suggested the notion of germinal continuity, and the conception is clearly expressed in his work already quoted: "The ovum gives rise to the divergent cells of the organism, but also to cells like itself. The ovarian ova of the offspring are these latter cells, or their direct unmodified descendants. The ovarian ova of the offspring share by direct inheritance all the properties of the fertilised ovum."

Galton.—The important theory of Galton now requires notice. Two preliminary notes are requisite. Galton was extremely doubtful in regard to the genuine inheritance of acquired characters. It was to account for the possible faint inheritance of some of these that he still admitted, as a subsidiary hypothesis, a limited amount of pangenesis. In the second place, it is needful to notice at the outset Galton's term "stirp," which he uses to express the sum-total of the germs, gemmules, or organic units of some kind, which are to be found in the newly fertilised ovum.

(1) Only some of the germs within the stirp attain development in the cells of the "body." It is the dominant germs which so develop.

(2) The residual germs and their progeny form the sexual elements or buds. The part of the stirp developed into the "body" is almost sterile. The continuity is kept up by the undeveloped residual portion.

(3) The direct descent is not between body and body, but between stirp and stirp. "The stirp of the child may

be considered to have descended directly from a part of the stirps of each of its parents, but then the personal structure of the child is no more than an imperfect representation of his own stirp, and the personal structure of each of the parents is no more than an imperfect representation of each of their own stirps."

Here it will be seen that there is a definite expression of the notion that the germinal cells of the offspring are in very direct continuity with those of the parents. The antithesis between the "soma" and the chain of germ-cells is emphasised.

Nussbaum.—The history must also include Nussbaum, who called emphatic attention to the very early differentiation and isolation of the sex-elements to be observed in some cases. The theory both of Jäger and of Nussbaum is that of a continuity of germinal *cells*. The theory of Weismann is more strictly that of the continuity of germinal *protoplasm*. The position of Jäger and Nussbaum may first be summarised more definitely:

(1) At an early stage in the embryo, the future reproductive cells of the organism are distinguishable from those which are forming the body.

(2) The latter develop in manifold variety, and lose almost all likeness to the mother germ.

(3) The former—the reproductive rudiments—are not implicated in the differentiation of the "soma," remain virtually unchanged, and continue the protoplasmic tradition unaltered.

(4) The sex-cells of the offspring being thus continuous with the parental sex-cells which gave rise to itself, they will in turn develop into similar products.

Now this fact of continuity of reproductive elements is obviously most satisfactory. If a fertilised egg-cell has certain characters, x, y, z, it develops into an organism in which these characters x, y, z are expressed; but, at the same time, the future reproductive cells are early set apart, retaining the

characters x, y, z in all their entirety, to start a new organism again with the same capital. Balbiani, who was not influenced by theoretical considerations, observed in *Chironomus* that the future reproductive cells were isolated before even the blastoderm was completed; that is to say, before almost any differentiation had occurred, a portion of the unspecialised ovum was insulated to continue the constancy of the species.

In this aspect the reproductive cells form a continuous chain, and the reproduction of like is as natural and necessary as it was in the Protozoa. No special theory is required. Similar conditions produce similar results. Unfortunately, however, a serious difficulty besets this easy theory. Such an early appearance and insulation of the reproductive cells, continuous with the very ovum itself, does indeed occur, and where it does the problem of heredity is simple. Early origin of special germ-cells, distinguished from those of the general "body," has been observed in some "worm-types" (leeches, *Sagitta*, threadworms, many Polyzoa) and in some Arthropods (*Moina* and *Cyclops* among crustaceans, not a few insects, Phalangidæ among spiders), while indications of the same early separation are not wanting in a number of other organisms. But it must be distinctly allowed that in most cases it is only after differentiation is relatively advanced that the future reproductive cells make their appearance. Thus we have to pass from the few cases as yet known of the continuity of the germinal *cells*, to the more general fact of the "continuity of the germ-plasma."

Weismann's Theory.—Weismann, like the previous investigators, had reached his conclusion independently. In the fact of continuity between the reproductive elements of generations, the solution of likeness must be found. But a direct chain of cellular continuity can only be said to exist in a few cases. The solution which is proposed for the majority of cases is as follows:

(1) "In each development a portion of the specific germinal

plasma (*Keimplasma*), which the parental ovum contains, is not used up in the formation of the offspring, but is reserved unchanged for the formation of the germinal cells of the following generation."

(2) What is actually continuous is the germ-plasm—" of definite chemical and special molecular constitution." A continuity of germinal cells is now rare; a continuity of intact germinal plasma is constant.

(3) This germ-plasm has its seat in the nucleus, is extremely complex in structure, but has nevertheless an extreme power of persistence and enormous powers of growth.

(4) "The germ-substance proper must be looked for in the chromatin of the nucleus of the germ-cell, and more precisely still in those ids or chromosomes which we conceive of as containing the primary constituents of a complete organism. Such ids in larger or smaller numbers make up the whole germ-plasm of a germ-cell, and each id in its turn consists of primary constituents or determinants, *i.e.* of vital units, each of which determines the origin and development of a particular part of the organism."

(5) "The splitting up of the substance of the ovum into a somatic part, which directs the development of the individual, and a propagative part, which reaches the germ-cells and there remains inactive, and later gives rise to the succeeding generation, constitutes *the theory of the continuity of the germ-plasm* which I first stated in a work which appeared in the year 1885" (1904, vol. i. p. 411).

CHAPTER XII

HEREDITY AND DEVELOPMENT

"To think that heredity will build up organic beings without mechanical means is a piece of unscientific mysticism."—WILHELM HIS. *But would even an omniscience of mechanical means explain the facts?*

§ 1. *Theories of Development*
§ 2. *Weismann's Theory of the Germ-Plasm*
§ 3. *Note on Rival Theories*
§ 4. *Weismann's Theory of Germinal Selection*

§ 1. *Theories of Development*

The Secret of Development.—In his forty-ninth exercitation on the "efficient cause of the chicken," Harvey (1578–1657), quaintly expressed his bewilderment before the baffling problem of development. "Although it be a known thing subscribed by all, that the fœtus assumes its original and birth from the male and female, and consequently that the egge is produced by the cock and henne, and the chicken out of the egge, yet neither the schools of physicians nor Aristotle's discerning brain have disclosed the manner how the cock and its seed doth mint and coine the chicken out of the egge." How much nearer a disclosure are we to-day? The visible sequences in the process of development are in many cases familiar, the external conditions of development are in many cases well known, and we have a little insight in regard to what is called the mechanics of development; but, on the whole, we have to confess that we

do not know the secret of development, which is part of the larger secret of life itself.

No doubt the process of development may be considered for certain analytical purposes as an orderly sequence of chemical and physical events. The developing embryo is the arena of intricate processes of chemical construction and disruption, of physical attractions and repulsions; but the characteristic feature of the whole business is, that it is co-ordinated, regulated and adaptive in a manner for which it seems at present, to say the least, very difficult to suggest any analogue in inanimate nature. For this reason not a few embryologists, such as Driesch, believe themselves warranted in frankly postulating a vitalistic factor—an Aristotelian "Entelechy."

An Outline of what is known.—We know that the germ-cells, and their nuclei more particularly, form the physical basis of inheritance; that there is a genetic continuity between the fertilised egg-cells which gave rise to the parents and those which gave rise to their offspring and those of their offspring; that fertilisation implies an intimate and orderly union of two individualities, condensed and integrated for the time being in the ovum and spermatozoon; that the sperm acts as a liberating stimulus on the ovum, as well as being the bearer of the paternal half of the inheritance and of a peculiar little body, (the centrosome), that plays an important part in the subsequent division of the fertilised egg-cell; that the mode of all development is by division of nuclei and the integration of the living matter into unit areas or cells, each presided over by a nucleus; that differentiation comes about very gradually—the obviously complex slowly arising out of the apparently simple; that paternal and maternal characteristics are distributed in exact equality by the nuclear or cellular divisions, and that the paternal and maternal contributions usually form the warp and woof of the web which we call the organism, and persist in the germ-cells thereof, though the expression or realisa-

tion of the bi-parental heritage varies greatly in each individual case; that the parental heritages include ancestral contributions which may be expressed in development or may lie latent; that normal development implies an appropriate environment, and that, during the development, there are subtle interactions between the growing organism and this environment, and between the different constituents of the growing organism; that the development is in certain aspects like the building-up of a mosaic out of many independently heritable and variable parts, and that it is in other aspects the expression of an integrated unity, with subtle correlations between the parts, and with remarkable regulative processes working towards an unconsciously predetermined end; that in a general way the individual development of organs progresses from stage to stage in a manner which suggests a recapitulation of the steps in racial evolution; that many items in the inheritance, presumed to be present because of their re-expression in subsequent generations, may lie latent and find no realisation in the individual development; that minute peculiarities of an ancestor may be handed on from generation to generation, although other peculiarities of that ancestor find no expression; that the offspring of two parents differing in regard to some well-defined character may all resemble one parent as regards that character; that the inbred offspring of these hybrids may have offspring divisible into two groups, one group resembling the one ancestor and the other group resembling the other ancestor; that in other cases the expressed inheritance seems as if it were a mosaic of ancestral contributions from parents, grandparents, great-grandparents in a diminishing geometrical ratio according to the remoteness of the ancestors: and we know much more than all this!

A Glimpse of our Ignorance.—On the other hand, we have still to confess our inability to solve the old problems: How are the characteristics of the organism potentially contained

within the germ-cells? how do they gradually find expression in development? what is the nature of the compelling necessity that mints and coins the chick out of a drop of living matter? what is the regulative principle that secures the order and progress which, by devious and often circuitous paths, results in the fully-formed organism?

The solution is still far off, and perhaps we shall never get beyond saying that a germ-cell has the power of developing, just as a crystal has the power of growing. But this need not hinder us from trying imaginatively to formulate what takes place, for it is largely through these provisional hypotheses that research is provoked and facts are won.

It may be said that there are two main ways of considering the fundamental problem of "individual becoming" which embryology raises, and as these are *analogous* to the theories of "Epigenesis" and "Evolutio" which were so much discussed in the seventeenth and eighteenth centuries, the same catch-words may be retained.

The Old Evolutio and Epigenesis.—Without going into the details of an often-repeated story, we may recall how men, like Bonnet (1720–93) and Haller (1708–77), maintained the preformation of the organism and all its parts within the germ. The egg, Bonnet said, contained *très en petit* the elements of all the organic parts. "*Es gibt kein Werden*," Haller said ("There is no becoming"). Those of this preformationist school regarded the apparent new formation of organs during development as an illusion; what occurs is only an unfolding (*evolutio*) of a preformed miniature. How the germ came to have this preformed miniature, they could not tell.

On the other hand, Caspar Friedrich Wolff (1733–94) was the pioneer of another school, in maintaining the reality of what he saw—a gradual differentiation from apparent simplicity to obvious complexity. The various organs of the developing embryo make their appearance successively and gradually,

and are to be seen being formed. There is no "evolutio"; there is *new formation* or "epigenesis." But how a germ that seems to start anew every time "from the pit of material homogeneity" can develop as it does, the upholders of epigenesis could not tell.

In fact, the preformationists and the believers in epigenesis came to a dead-lock, and both schools usually fell back on the assumption of hyperphysical agencies. Until the genetic or germinal continuity which links generation to generation was realised, there could be no real progress in theories of development.

The New Evolutio and Epigenesis.—With the growth of embryology the whole venue has changed, and it would be misreading history to say that students of development are still facing the dilemma expressed in the opposition between the eighteenth-century schools of evolutio and epigenesis. Yet there is to-day an *analogous* antagonism, which we must briefly discuss.

The Mosaic Evolutio Theory.—On one view it is supposed that the germ-cell has an architectural organisation, predetermined before development begins, and that development is in part a "histogenetic sundering" of the pre-existing germinal mosaic. Some authorities have suggested that the predetermination is in the organisation of the egg-cytoplasm—the central idea of the theory of "organogenetic germinal areas" which His elaborated in 1874. This theory may find support in experiments such as those of Roux on the frog ovum, in which one of the first two cleavage-cells was punctured, and its intact neighbour developed into a *one-sided* embryo; though the edge is taken off this case by the observation of Hertwig that in *other* conditions the intact blastomere may develop into a complete embryo of half the normal size. T. H. Morgan has shown that if the ova experimented with are kept stationary the result observed by Roux is likely to be seen, while if they are allowed free movement in the water the result observed

by Hertwig is likely to be seen. The theory may find support in the experiments of Morgan and Driesch on Ctenophore ova, where a defect in the cytoplasm (not involving the nucleus) is often followed by a modified cleavage and a defective embryo, as if the architecture had been seriously injured; but it may be opposed by Delage's experiments on merogony, where a small (and non-nucleated) fragment of a sea-urchin's egg may be fertilised and give rise to a complete larva. In some cases like the last it seems impossible to maintain that different parts of the egg are predetermined in relation to particular structures, and the same conclusion is suggested by Wilson's experiments on the lancelet ovum, where an isolated blastomere of the four-cell stage develops into a complete larva. In other cases, however, it *seems* as if the egg had a fixed and set architecture, which cannot be damaged without affecting the embryo. In certain cases there is proof that the egg contains pre-formed, and even pre-localised, organ-forming substances, and the removal of a small part may be followed by the absence of a definite structure, should development go on. In some cases it seems clear that the old view of the ovum as homogeneous and isotropic must give way before experimental evidence of heterogeneity.

The "Preformation" mainly Nuclear.—But the researches of Kölliker, Strasburger, Hertwig, and others led to a transference of attention from the cytoplasm of the germ-cell to the nucleus. From the importance of the nucleus in metabolism, in the regeneration of Protozoon fragments, in maturation, in fertilisation, and in cleavage, it was argued—most forcibly, perhaps, by Weismann—that the nucleus must be the bearer of the heritable qualities. Meanwhile, many were recognising the value of Nägeli's conception (1884) of a specific idioplasm—a complex substance which, in its molecular organisation and in the metabolism it induces, is different for each species. Weismann developed this in his theory of the germ-plasm, which he regarded as wholly

resident in the chromosomes of the nucleus. Thus, the locality of the pre-established organisation was shifted from the cytoplasm to the nucleus, but it is not inconsistent with this to suppose that the essential mosaic or organisation within the chromosomes of the nucleus may induce a secondary mosaic or localisation in the building material which the general substance of the egg-cell affords. It need hardly be pointed out that the organisation or architecture which is thought of in such cases is something infinitely finer than the microscopically visible (reticular or alveolar) structure which all living matter exhibits.

What is Distinctive in Development?—Unicellular organisms divide and redivide rapidly; it is their normal mode of multiplication. The germ-cells of multicellular animals do the same in the early chapters of their history. The fertilised egg-cell does the same; but the daughter-cells or blastomeres cohere to form an embryo, just as the daughter-cells into which some Protozoa divide also cohere to form a "colony." For a time there is no growth among the cleavage-cells into which the fertilised ovum divides, so that an embryo of sixty-four cells or more is no larger than the undivided egg. This, again, is paralleled by cases of spore-formation in Protozoa, where many divisions occur in a short time and within the limited space of the mother-cell. In some cases the young embryo shows a large number of nuclei derived from the division of the fertilised nucleus of the egg-cell, while the cell-substance is slow in being segregated around the nuclei into unit-areas or cells. This, again, is paralleled by some multinucleate Protozoa.

Thus the really distinctive fact in development is the progressive differentiation. The daughter-cells do not remain homogeneous; some start a lineage of nerve-cells, others a lineage of digestive cells, and so on. In a gradual, orderly fashion the apparently simple gives rise to the obviously complex, and throughout the process there are striking phenomena of adjustment to temporary conditions, of "self-differentiation"

on the one hand and mutual influence on the other, and of integrated "regulation" throughout. We are so familiar with the orderly succession of events that we hardly realise the marvel of it, until we play some trick with the developing egg, introducing disorder, and see how equilibrium and normality are restored. Thus the one-sided half-embryo of the frog proceeds at a certain stage to develop the missing half.

Roux.—Starting from the assumption that the nuclei of the germ-cells contain a specific idioplasm or architectural substance (the vehicle of the heritable qualities), and with the further assumption that this substance is a complex aggregate of different kinds of particles (the material expressions of the different sets of qualities), Roux invented the hypothesis of two kinds of nuclear division, *quantitative* and *qualitative.* The former results in equivalent, the latter in dissimilar nuclei; the former is an integral, the latter a differential division. Roux supposed that the latter mode was characteristic of the early stages of development, during which the different components or qualities of the idioplasm are distributed among the blastomeres. Thus it comes about that each blastomere, though not independent of its neighbours, is endowed with a power of "self-differentiation" along particular lines defined by its specific share of the idioplasm.

Weismann.—Similarly, but even more elaborately, as we shall see, Weismann pictured development as a gradual process of differential division, distributing the representative particles or primary constituents of the germ-plasm. While this is going on there is also a process of quantitative division, which gives rise to the lineage of future germ-cells bearing the complete equipment of germ-plasm, and this quantitative division also occurs amid the qualitative divisions when many cells with identical characters are produced.

Criticism of Mosaic Theories.—These mosaic theories of development have been criticised from many sides. Thus it is

pointed out that no visible phenomena of nuclear division suggest that the partition may be *qualitative*; on the contrary, that the whole elaborate process of nuclear division seems adapted to secure the exact equivalence of the two daughter-nuclei. It may be, however, that while there is always a general equivalence, in the sense, for instance, that the large nuclear bodies or chromosomes are accurately split, and that each daughter-cell gets the same number, there may be at the same time a more intricate qualitativeness in the division. Again, the critics have brought forward some of the results of experimental embryology which seem at first sight to tell against the hypothesis of differential division, especially where one of the first two or first four blastomeres is seen to form a complete and normal embryo, or where under artificial conditions (of pressure, etc.) certain cells develop into tissues which in normal conditions are formed by quite different cells. To explain these and other difficulties—*e.g.* regenerative phenomena—various ingenious sub-hypotheses have been invented. It seems highly probable that the distribution of particular characters (if it be a reality at all) occurs sooner in some developing eggs than in others; in other words, that the cells of some embryos are "set" and defined at an earlier date than those of other embryos.

Non-Mosaic Theories.—All embryologists agree that a germ-cell has a specific organisation, but many will not admit that it is necessary or useful to people the nucleus with a large body of representative particles, ready to distribute themselves and work upon the virgin soil which the protoplasm affords. All agree that there is gradual differentiation of cells as development proceeds, but many will not admit that it is necessary or useful to think of this in terms of a distribution of representative particles from the original depot in the nucleus of the fertilised egg-cell.

Oscar Hertwig may be named as a prominent representative of those who give the facts of development an interpretation somewhat different from that suggested by Roux and Weismann.

We may suppose that, from the youngest ovarian ovum onwards, the nucleus exerts a " control " upon the surrounding cytoplasm, whether by the migration of "pangens" (De Vries), or of specific formative substances (Sachs), or of enzymes, or by a propagation of molecular movements (Nägeli). In some such way—varying greatly in degree in different cases—the nucleus prepares in the cytoplasm of the egg a framework for its future operations. This may be so slightly pre-established that from a minute fragment of the egg a complete larva may be reared (as in sea-urchins), or so well established that if a part of the unsegmented egg be removed the remainder forms a defective larva (ctenophore).

The nucleus of the fertilised egg-cell divides into equivalent halves, but these find themselves in more or less different territory, as the result of the preparatory framework which the nucleus, before division, had established in the cytoplasm. In technical language, the nuclei, though equivalent, find themselves in a not altogether isotropic medium.

The dividing nuclei, as Driesch and Boveri suggest, are differently stimulated to expression in the different areas of the heterogeneous cytoplasm, and they thus call forth new differentiations in these, in ever-increasing complexity of action and reaction.

If the initial cytoplasmic differentiation was slight, the first steps in differentiation will be correspondingly slight, and in these cases an isolated cleavage-cell or blastomere may still form a complete embryo, as in the lancelet. If the initial cytoplasmic differentiation was more pronounced, an isolated blastomere may not be able to do more than form a partial embryo; the "setting" of the cytoplasm may be too strong to be overcome even by the completely equipped blastomere-nucleus.

Thus we reach the idea, expressed, for instance, by Driesch, that " the relative position of a blastomere in the whole determines in general what develops from it; if its position be changed, it gives rise to something different; in other words, *its prospective*

value is a function of its position." But the "position" has a more than merely topographical connotation; it means, as Prof. E. B. Wilson says, "the physiological relation of the blastomere to the inherited organisation of which it forms a part."

But, here again, even when we recognise as fully as we can (*a*) the importance of the initial inherited organisation, (*b*) the influence of segment upon segment as development proceeds, and (*c*) the continually operative influence of the normal environmental stimuli, we have still to confess that the process of development remains very mysterious.

The Antithesis of the Two Views.—The student who is not yet clear as to the antithesis of the two views of development outlined above should read Dr. Chalmers Mitchell's admirably lucid introduction to his translation of Prof. Oscar Hertwig's *Biological Problem of To-day* (London, 1896). It concludes with the following contrast: "Hertwig says that all the cells of the epiblast, hypoblast, mesoblast, and of the later derivatives of these primary layers receive identical portions of germ-plasm by means of doubling [quantitative or integral (*erbgleich*)] divisions. The different positions, relations to each other and to the whole organism, and to the environment in the widest sense of the term, cause different sides of the capacities of the cells to be developed; but they retain in a latent form all the capacities of the species. Weismann says that the nuclear divisions are differentiating [qualitative (*erbungleich*)], and that the microcosms of the germ-plasm, in accordance with their inherited architecture, gradually liberate different kinds of determinants into the different cells, and that, therefore, the essential cause of the specialisation of the organism was contained from the beginning in the germ-plasm."

That differentiation may occur at very early stages is certain; that it has potentially occurred, although there is no visible evidence of it, is also certain; it seems to us difficult to interpret this without the hypothesis of differential division.

At the 2-cell or 4-cell stage of the development of the egg of the sea-urchin, the cells are equipotential, for an isolated blastomere (even at the 8-cell stage) may develop into a complete larva (Driesch).

But a little later, when invagination has occurred, when two germinal layers are established, the cells are no longer equipotential.

They can no longer regenerate complete larvæ. Even when several cells are separated off, they are not able to develop into complete larvæ. They grow into monstrous forms, which soon die. It is difficult to see why this should be so, unless differential division has occurred.

An Analogy.—A well-organised body of colonists reaches a new land, which they will develop. Soon after they land they distribute themselves in bands, according to their bent, as hunters, shepherds, fishers, farmers, miners, and so forth. As they possess the new land more and more fully, they segregate more and more, dividing into increasingly specialised bands; and as these find themselves in appropriate areas they settle down, and they stamp the areas with their particular character. Here a farm arises and there a factory, here a sheep-ranch and there a store, here a mine and there a fishing village. We can quite well understand that certain interpreters or historians would lay emphasis on the fact that, as the emigrant bands journeyed, they segregated persistently into smaller and more specialised groups, according to the old-established—indeed hereditary—predispositions or qualities of the members composing the bands. This is a far-off image of the mosaic theory of development with its hypothesis of differential divisions.

On the other hand, we may imagine another well-organised body of colonists reaching another new land, which they will develop. They have a complex organisation with many potentialities, and they work best together. It cannot be said that some are preformed to be hunters, others to be shepherds, others to be fishers, others to be farmers, others to be miners, and so on. They begin by marking out the surrounding area into localities, and into each locality a representative band of emigrants proceeds to journey. They divide into homogeneous bands, each with a full representation of the capacities of the original body of colonists. But as they spread they are necessarily influenced by the area in which they find themselves.

and by their relations to neighbouring bands, and gradually they, too, differentiate into distinctive kinds of settlements. We can quite well understand that certain interpreters or historians would lay emphasis on the fact that, as the originally similar bands of colonists journeyed, they became differentiated in response to the varied environmental conditions and in relation to their neighbours. Their prospective value at any moment is "a function of their locality." This is a far-off image of the non-mosaic theory of development. *It is surely conceivable that both interpretations are correct.*

Summary.—According to the mosaic theory, the main mode of differentiation is *qualitative* nuclear division, which sifts out the various items of the mosaic (the representative particles or primary constituents) into different cells. Thus, if the fertilised ovum had the qualities or potential qualities *abcxyz*, its first four daughter-cells or blastomeres might have the qualities *abcxyz*, *abxyz*, *abcxy*, and *abcxz*. What each cell becomes is primarily determined by the particular contingent of representative particles which possesses it.

According to the non-mosaic theory, the division of the nucleus is always *quantitative*—*i.e.* without any sifting out of particular potentialities—and differentiation is due to the varied relations in which the nuclei find themselves. The prospective value of an embryonic cell, Driesch said, is "a function of its location." Each of the early cells is supposed to have a complete set of specific characteristics *in potentia*; but some of these remain latent, while others become active, this being determined by the relations of the cell to the whole system of which it forms a part.

Thus, while the two views agree in attributing to the essential germinal material a specific organisation corresponding to the hereditary qualities, they differ in their picture of what differentiation implies, the mosaic theory relying on the hypothesis of qualitative division which segregates representative particles,

the non-mosaic theory denying qualitative division and emphasising the importance of environmental interaction in the widest sense.

It must be carefully noted that as far as the eye can see, there is in the development of the embryo *only one kind of cell-division,* which involves a visibly accurate longitudinal halving of each of the chromosomes of the nucleus. Therefore if there is any qualitative or differential division it must be of a subtler sort.

§ 2. *Weismann's Theory of the Germ-plasm*

No one has done more to further the scientific study of heredity than Prof. August Weismann, of Freiburg, although his work has been on different lines from that of the statistical school which we particularly associate with the names of Mr. Francis Galton and Prof. Karl Pearson, or from that of the experimental school which we particularly associate with the names of Gregor Mendel and Mr. Bateson. In general we may say that Weismann has thought out a *theory of heredity,* coherent with a theory of development and a theory of evolution, which has inspired much research and has commanded the admiration of his most resolute opponents. He has done for the study of heredity what Dalton with his atomic theory did for chemistry, and though his theory will doubtless be developed, as Dalton's has been, it seems unlikely that the fundamental ideas of Weismannism will be discredited in the future evolution of biology.

As Weismann's interpretations have gone on growing as facts accumulated and as his insight increased, they present difficulty to those who have not followed their development, and it is therefore necessary to present a brief statement of Weismannism as developed, for instance, in *The Evolution Theory* (1904).

The Material Basis of Inheritance.—It seems that the botanist Nägeli was the first to point out that the material basis on which the hereditary tendencies depend must be a *minimal* quantity of substance. The inheritance from the father and from the mother is potentially equal; the vehicle of this inheritance is in the germ-cells; the mass of a spermatozoon may be only $\frac{1}{1000000}$th part of the mass of the ovum which it fertilises; in one respect the two sex-cells are equivalent —they have the same number of stable readily stainable bodies or chromosomes in their respective nuclei; the number of these bodies is constant for each species, except that the number in the mature sex-cells is half that found in the ordinary cells of the body; the chromosomes play an obviously important part in the intermingling or amphimixis which occurs in fertilisation and in the subsequent divisions of the fertilised egg: for these and other reasons, Weismann concluded in 1885, as Strasburger and O. Hertwig did about the same time, that *the hereditary substance is in the chromosomes of the nucleus of the germ-cell.*

Microscopic vivisection experiments on Protozoa—*e.g.* the trumpet animalcule, *Stentor*—show that a fragment of a cell with a portion of nucleus will live on and reconstruct an entire organism, whereas a portion without nucleus, though it lives for a time, is unable to assimilate or recuperate its losses and soon dies. "It is in the nucleus, therefore, that we have to look for the substance which stamps the material of the cell-body with a particular form and organisation—namely, the form and organisation of its ancestors." It goes without saying that the sex-cell is a unity, a minute organism, that its cell-protoplasm (in the case of the ovum at least) represents the building-material (trophoplasm), in which alone the hereditary substance (idioplasm) can unfold its wonderful powers; but it must be remembered that even a non-nucleated fragment of an ovum may develop (into a larva at least) if it be fertilised—*i.e.* supplied

with a sperm-nucleus. *Everything points to the conclusion that there is a definite hereditary material, and that it is in part at least bound up with the chromosomes of the nuclei of the paternal and maternal germ-cells.*

The Germ-plasm mainly Nuclear.—No one can doubt that a germ-cell is a unity, that it represents a "cell-firm," that its virtue is dependent on the interaction of nucleoplasm, cytoplasm, and centrosome, or that the substance of the egg is the actual building-material out of which the embryo is constructed. And yet, there are many facts which compel us to conclude that the basis of inheritance is essentially bound up with the chromosomes of the nucleus. Repeating, in part, what we have said in Chapter II., we may note the following facts:

1. In some cases almost the whole cytoplasmic differentiation of the spermatozoon—namely, the locomotor apparatus—is left outside the ovum, and what enters is the head, which is almost purely chromatin-material, plus the minute mid-body or centrosome, which functions as a dynamic centre in division.

2. The chromatin-bodies or chromosomes have a constant number for each species, except that in the mature sex-cells the number is half the normal, *i.e.* half the number found in the body-cells.

3. In nuclear division the chromosomes are longitudinally split, and are in various ways so distributed that each of the daughter-cells into which a mother-cell divides receives a precisely equivalent quota of chromosomes.

4. In many cases it is certain that the chromosomes of the spermatozoon entering the ovum are precisely equivalent in number to those which the mature ovum contains.

5. Throughout the whole world of life, the chromosomes—whether during the growth, or the maturation, or the amphimixis of germ-cells—behave in a generally similar manner, though there are many differences in detail.

Ancestral Plasms.—Assuming that the chromatin substance of the nucleus of the germ-cell is the vehicle of the inheritance, Weismann argued that it "contains not only the primary constituents of a single individual of the species, but also those

of several, often even of many, individuals." In fact it is a mosaic of "ancestral plasms." But what evidence is there of this?

A fertilised egg develops into an organism by cell-division. For a time it is demonstrable that the nucleus of each of the daughter-cells into which the fertilised egg-cell divides contains paternal and maternal chromosomes in equal number. Gradually differentiation sets in, and various kinds of body-cells with specialised structure and function appear; but often it is quite demonstrable that the maternal and paternal contributions are forming the warp and woof of the organism. While most of the ever-increasing crowd of embryonic cells undergo differentiation, some do not, but remain unspecialised, retaining the characters of the fertilised ovum. From this lineage of unspecialised cells, as we have explained in Chapter II., the germ-cells of the new organism arise. By-and-by when the organism becomes mature, these germ-cells are liberated, and each of them will have, by hypothesis, chromosomes derived from the original father and mother. But fertilisation will occur between these liberated germ-cells and others whose chromosomes are likewise derived from another father and mother, assuming that the usual cross-fertilisation occurs. Thus there comes to be an accumulation of contributions from different ancestors, though the actual number of visible stainable bodies or chromosomes is always kept the same. *It seems impossible to evade the conclusion that the material basis of inheritance is a mosaic of ancestral plasms.*

It is interesting to recall Darwin's memorable saying: "Each living creature must be looked at as a microcosm—a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars in heaven." He thought of his hypothetical gemmules as including not merely the contributions of the immediate parents, but ancestral items from even remote progenitors.

As a non-nucleated fragment of egg fertilised by a sperm will in some cases—*e.g.* sea-urchins—develop into a normal larva, as an unfertilised ovum—*e.g.* of sea-urchin—may under certain treatment develop into a normal larva, it is obvious that each of the germ-cells has in its nucleus a complete set of hereditary qualities.

As a single egg often produces two complete organisms (true twins), and in some cases—*e.g.* the parasitic Hymenopteron *Encyrtus*—produces a legion of embryos, it is obvious that, however the hereditary qualities are contained in their chromatin vehicle, they can be very readily and rapidly multiplicated by division; and every one is aware how many germ-cells can be produced in a short time by a sexually mature animal.

It is now well known for a large number of animals and plants that during the maturation of ovum and spermatozoon the number of chromosomes is reduced to half the normal number characteristic of the body-cells of the species, so that the union of sperm-cell and egg-cell results, not in a doubling of the usual number of chromosomes (as would be the case were there no reduction), but in a restoration of the normal number. It therefore follows that a reduction of the number of chromosomes by a half does not in any way affect the completeness of the heritage. "The halved hereditary substance still contains the whole mass of primary constituents."

By following up this line of argument, Weismann was led to the theoretical conclusion that each of the chromosomes must contain a complete equipment of hereditary constituents, and that the germ-plasm represented by all the chromosomes in the germ-cell must include several "complexes of primary constituents," each complex sufficient in itself to form a complete individual. In other words, the fertilised egg-cell is a mosaic of "ancestral plasms."

"I call the idioplasm of the germ-cells *Germ-plasm*, or the

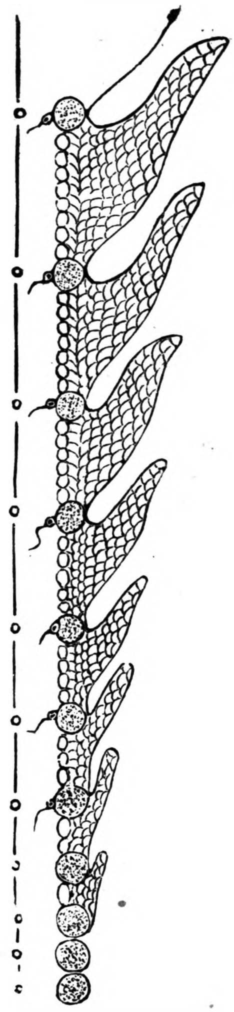

FIG. 43.—The relation between reproductive cells and the "body." The broken vertical line to the left represents a succession of ova from which "bodies" are produced. The other part of the figure indicates a chain of "bodies,"—successive generations. For convenience of the diagram, the "bodies" are represented as if larger at each generation. A sperm fertilising an ovum at the beginning of each generation is indicated.

primary-constituent-substance of the whole organism; and the complexes of primary-constituents necessary to the production of a complete individual I call *Ids*." [In some cases these "ids" are probably the chromosomes, but many band-like chromosomes (or "idants") are visibly compound, consisting of several ids.] It is through the co-operation of these ids that the precise constitution of the individual which develops from the fertilised ovum is determined.

Every one admits that the germ-cell has a complex organisation, with the details of which every year makes us better acquainted. Every one admits that the whole substance of the fertilised ovum cannot be equally important as regards inheritance. Every one admits that small but still visible units—the ids or the chromosomes—behave as if they were of fundamental importance. If we admit that there is a hereditary substance at all, the theoretical interpretation begins when we regard these ids as containing a com-

plete set of hereditary qualities, as containing implicitly all the parts of a perfect animal, as the units in that multiplicate mosaic which makes up an inheritance.

There is more than a superficial resemblance between this doctrine and the Buddhistic theory of Karma. As Huxley said, "the tendency of a germ to develop according to a certain specific type is its Karma. It is the 'last inheritor and the last result' of all the conditions that have affected a line of ancestry which goes back for millions of years to the time when life first appeared on the earth. The germ-plasm is the last link in a once continuous chain extending from the primitive living substance; and the characters of the successive species to which it has given rise are the manifestations of its gradually modified Karma." (See *Evolution and Ethics*.)

Determinants.—"I assume," Weismann says, "that the germ-plasm consists of a large number of different living parts, each of which stands in a definite relation to particular cells or kinds of cells in the organism to be developed—that is, they are 'primary constituents' in the sense that their co-operation in the production of a particular part of the organism is indispensable, the part being *determined* both as to its existence and its nature by the predestined particles of the germ-plasm. I therefore call these last *Determinants*, and the parts of the complete organism which they determine *Determinates*" (1904, vol. i. p. 355).

But how many determinants are to be postulated in any given case? Weismann supposes that every independently variable and independently heritable character is represented in the germ-plasm by a determinant. A lock of white hair among the dark may reappear at the same place for several generations; it is difficult to interpret such facts of particulate inheritance except on the theory that the germ-plasm is built up of a large number of different determinants.

It may be pointed out that almost all biologists who have

tried to form a conception of the ultimate structure of living matter have been led to the assumption—expressed in very varied phraseology—of ultimate protoplasmic units which have the powers of growth and division. It is in no way peculiar to Weismann to imagine biophors and to credit them with the powers of growing and dividing. This cannot, indeed, be proved, but many facts point to it. The cell divides, but this is preceded by the division of the nucleus; the nucleus divides, but this involves splitting of the chromosomes; and the chromosomes are sometimes visibly composed of still smaller bodies, arranged like beads on a string. As Prof. E. B. Wilson says (1900, p. 84), "Our study of nuclear division reveals to us, not a homogeneous dividing mass, but a descending series of dividing elements, which, as if seen through an inverted telescope, recede from the eye almost to the limits of microscopical vision. There is no reason to place the limit of this series at the point where it vanishes from view, and we are thus almost irresistibly driven to the conclusion that the division of the nuclear substance as a whole must be the result of division on the part of invisible elements, by the aggregation of which the visible structures are formed." Moreover, in many cases the cytoplasm or extra-nuclear part of the cell contains minute bodies or "plastids"—*e.g.* chlorophyll corpuscles—which also multiply by division.

Those who find it difficult to believe in the theory that there are multiple sets of analogous determinants in the germ-plasm should consider, for instance, the facts of sex and sexual dimorphism. A queen bee lays an unfertilised egg which develops into a drone or male, which is in many detailed ways different from the queen, and is primarily different in producing spermatozoa, not ova. But since this drone has only a mother, no father, there must have been in the fertilised ovum which developed into the mother-bee the potentiality—*i.e.* the determinants—of male reproductive organs and masculine characters.

Yet there was no hint of these in the queen bee herself. They must have lain as latent elements in her inheritance. In the case of plant-lice (Aphides) and some water-fleas (Daphnids), where there is a succession of parthenogenetic females, the primary constituents of masculine characters must remain latent for several generations. In some cases—*e.g.* sea-urchins—the sexes are so closely alike, even as regards their reproductive organs, that we may almost say that they differ only in 'physiological gearing,' and that to postulate one army of determinants is sufficient without complicating matters by postulating at least two analogous armies. But in the great majority of cases there is marked dimorphism between the sexes, and, even in the cases above referred to, it has to be remembered that the spermatozoon itself is a very complex structure, with apical piece, head, middle piece, tail, and other minutiæ, many of which have no analogue in the ova, and are, indeed, specially adaptive peculiarities which aid the spermatozoon in finding the ovum. Thus it is difficult to escape Weismann's conclusion that both kinds of sexual characters must be present, some active, some latent, in every germ-cell and in every organism.

Another good example may be found in wheel-animalcules or Rotifers, where the primitive germ-cells divide into two kinds of eggs, externally identical, and yet so different that from the one kind only females develop, and from the other kind only males. Neither kind is fertilised. The ova which develop into females must carry with them determinants corresponding to masculine characters, though these remain quite latent, for these females give origin to males as well as females. It may be that nutritive and other environmental influences determine whether the determinants corresponding to the female sex or those corresponding to the male sex become active; but the point at present is, that it is difficult to think out what occurs except on the hypothesis that the germ-plasm

contains both male and female determinants, analogous but distinct.

Summary of Weismann's View.—"The germ-substance owes its marvellous power of development not only to its chemico-physical constitution, but to the fact that it consists of many and different kinds of primary constituents--that is, of groups of vital units equipped with the forces of life, and capable of interposing actively and in a specific manner, but also capable of remaining latent in a passive state until they are affected by a liberating stimulus, and on this account able to interpose successively in development. The germ-cell cannot be merely a simple organism; it must be a fabric made up of many different organisms or units—a microcosm" (1904, vol. i. p. 402).

A living creature usually takes its origin from a fertilised egg-cell, from a union of an ovum and a spermatozoon—two dimorphic germ-cells. These germ-cells are descended by continuous cell-division from the fertilised ova which gave rise to the two parents; they have retained the organisation of those fertilised ova, and this organisation has its vehicle in the stainable material of the nuclei—the germ-plasm. This germ-plasm consists of several chromosomes or idants, each of which is made up of several pieces or ids, each of which (here hypothesis begins), is supposed to contain all the potentialities—generic, specific, and individual—of a new organism. Each id is a microcosm with an architecture which has been elaborated for ages; it is supposed to consist of numerous determinants, one for each part of the organism that is capable of varying independently or of being independently expressed during development. Lastly, each determinant is pictured as consisting of a number of ultimate vital particles or biophors, which are eventually liberated in the cytoplasm of the various embryonic cells. All these units of various grades are capable of growth and of multiplication by division.

Summary.

The physical basis of inheritance—the germ-plasm—is in the chromatin of the nucleus of the germ-cell.

The chromatin takes the form of a definite number of chromosomes (or idants).

The chromosomes consist of ids, each of which contains a complete inheritance.

Each id consists of numerous primary constituents or determinants.

A determinant is usually a group of biophors, the minutest vital units.

The biophor is an integrate of numerous chemical molecules.

Maturation and Amphimixis.—It is necessary here to interpolate a reference (*a*) to the facts of maturation—the processes that occur in the immature egg-cells (oocytes) and in the immature sperm-cells (spermatocytes); and (*b*) to the facts of amphimixis or fertilisation—the intimate and orderly union of the (reduced) nuclei of the two kinds of sex-cells.

Since the spermatozoon is known to bring into the mature ovum the same number of chromosomes as the mature ovum contains in its nucleus, each act of fertilisation would double the *normal number* of chromosomes if there were not some process obviating this. The doubling of the normal number does not occur, because the mature spermatozoon and the mature ovum have already undergone a reduction of the number of their chromosomes to half the normal number.

In various ways, during the divisions of the sperm-cells antecedent to their complete differentiation, and during the process which is called the maturation of the ovum—the two divisions which result in the liberation of two polar bodies—the normal number of chromosomes is reduced by a half. Thus, when fertilisation occurs, the number of chromosomes is restored to the normal. This fact has been securely established by the researches of Van Beneden, Oscar Hertwig, Boveri, Henking, and others.

Reducing Divisions.—Since Van Beneden discovered that

each of the two nuclei which unite in fertilisation contains one-half of the number of chromosomes characteristic of the somatic cells, though the nuclei of the earlier stages of the germ-cells have the same number as the somatic cells, it has been plain that a reducing process must occur at some stage, and there is now general agreement that the reduction takes place in the last two cell-divisions by which the definitive germ-cells arise—namely, when the ovarian ovum gives rise to the mature ovum and two or three

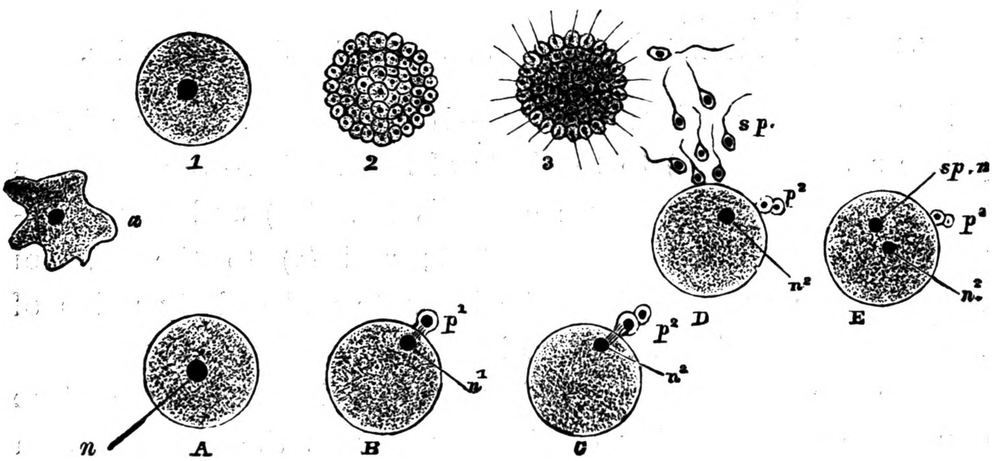

Fig. 44.—Diagram of maturation and fertilisation. (From *Evolution of Sex.*)

The upper line shows development of spermatozoa. The lower line shows maturation of the ovum. The middle line to the right shows fertilisation. *a*, an amœboid primitive sex-cell; A, ovum, with nucleus or germinal vesicle (*n*); B, ovum, liberating first polar body (p^1); C, extrusion of second polar body (p^2); 1, a mother-sperm-cell or spermatogonium; 2, 3, balls of immature spermatozoa, resulting from the division of (1); *sp.*, mature spermatozoa; D, the entrance of a spermatozoon into the ovum; E, the male and female nuclei *sp.n* and n^2, approach one another.

polar bodies, and when a spermatocyte divides into four spermatids or young spermatozoa. The parallelism in the two cases is very striking, but as O. Hertwig says, " while in the latter case the products of the division are all used as functional spermatozoa, in the former case one of the products of the egg-mother-cell becomes the egg, appropriating to itself the entire mass of the yolk at the cost of the others, which persist in rudimentary form as polar bodies." The hypothesis of Minot, adopted also by

Van Beneden, that each germ-cell is originally hermaphrodite, and that the maturation processes imply the removal of male qualities from the ovum and of female qualities from the spermatozoon, has been abandoned ; and the reducing divisions are recognised as securing a constancy in the number of chromosomes characteristic of each species, for without some such preliminary reduction the number would obviously be doubled at each fertilisation. That a reduction does really occur in both plants and animals seems now incontrovertible, but the precise manner of the reduction seems to differ considerably in different organisms.

Reduction in Parthenogenetic Ova.—There is an interesting variety of occurrence.

(*a*) In ants, bees, and wasps, all the ova (with 2N chromosomes to start with) undergo reduction, the number of chromosomes being halved (N). Some ova are unfertilised and these develop into males, whose cells have therefore half the normal number of chromosomes (N). There is no reduction of the chromosomes in the making of the sperms. Thus when a spermatozoon (with N chromosomes) fertilises a reduced ovum (with N chromosomes) the normal number, 2N, is restored, and the resulting female retains that number.

(*b*) In Rotifers and some water-fleas (*e.g. Daphnia*) parthenogenesis occurs when the nutritive and other conditions are favourable, and only females are produced. The ova do not undergo reduction, but retain the normal number of chromosomes (2N). In unfavourable conditions eggs of two sizes are produced, and both undergo reduction. The small ones, with N chromosomes after reduction, are not fertilised, and develop into males. The large ones, also with N chromosomes after reduction, are fertilised, and develop in the 2N condition into females.

(*c*) In Aphides or plant-lice, parthenogenesis is the rule in favourable conditions ; reduction does not occur, and females are produced. In unfavourable conditions males appear. Some of the eggs undergo ordinary reduction (to N), and being raised to the 2N condition by fertilisation develop into females. Other eggs produced in unfavourable conditions undergo a *partial* reduction to 2N − 1, or 2N − 2, are not fertilised, and develop into males. In the formation of the male-cells there are some with N − 1 chromosomes and some with N chromosomes, but the former degenerate and only the latter become effective spermatozoa.

Minute inquiries have gone so far that it is possible to assert that in some cases the young germ-cell has an equal number of paternal and maternal chromosomes. And similar minute inquiries—which almost baffle us with their intricacy—make it exceedingly probable that in the reduction divisions maternal chromosomes separate from paternal chromosomes, and yet not so thoroughly that all the paternal chromosomes pass into one cell and all the maternal into another. If this be true, we can better appreciate the importance of the reduction-divisions which occur in maturation, for they afford opportunity for new permutations and combinations of hereditary qualities. They do not originate anything new, but they shuffle the cards, so to speak.

Fertilisation.—Recent work has forcibly suggested that there are in fertilisation two more or less distinct processes: on the one hand, the process by which the gametes, bearing the hereditary characters, unite to form the beginning of a new individuality; on the other hand, the process by which the spermatozoon supplies some stimulus, prompting the ovum to divide. The first aspect is that of amphimixis, believed by many to be of importance in initiating—and, it may be, also in checking—variations, but in any case effecting the union of hereditary qualities contained in the two gametes. The second aspect is that of mitotic stimulus, believed by some to be afforded by an enzyme—for which the name of "ovulase" has been suggested —and by others to be localised in the sperm-centrosome. It is seen in many cases that equivalent numbers of chromosomes are contributed by the two nuclei; it is evident that the ovum contributes by far the larger quantity of cytoplasm; it seems to have been securely demonstrated in some cases that "from the father comes the centrosome to organise the machinery of mitotic division by which the egg splits up into the elements of the tissues, and by which each of these elements receives its quota of the common heritage of chromatin." "Huxley hit the mark two-score years ago when he compared the organism

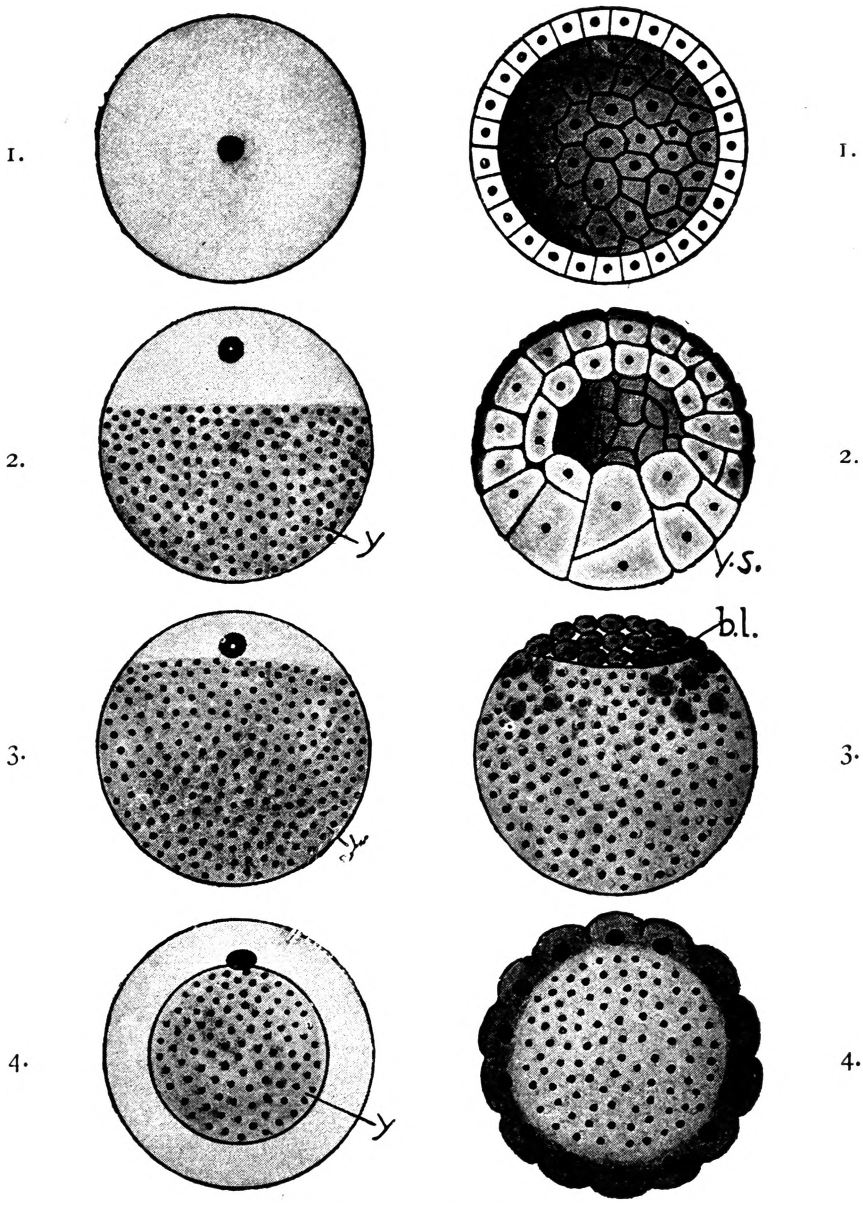

FIG. 42.—Modes of segmentation.

1, Ovum, with little yolk, segments wholly and equally into a ball of cells (blastula), *e.g.* sea-urchin ; 2, ovum, with a considerable quantity of yolk (*y*), segments wholly but unequally, *e.g.* frog ; *y.s.* larger yolk-laden cells ; 3, ovum, with much yolk (*y*) towards lower pole, segments partially and discoidally, forming blastoderm (*bl.*), *e.g.* bird ; 4, ovum, with much central yolk (*y*), segments partially and peripherally, *e.g.* crayfish.

[*Facing p.* 438.

to a web, of which the warp is derived from the female and the woof from the male. What has since been gained is the knowledge that this web is to be sought in the chromatic substance of the nuclei, and that the centrosome is the weaver at the loom" (Wilson, 1896, p. 171). While the ovum-centrosome of many animals seems to disappear, that introduced by the spermatozoon divides into two, and around each a system of rays develops. The sperm-centrosomes migrate to opposite sides of the segmentation nucleus, and between them appears the spindle of the first cleavage. It may be hasty to call them "kinetic centres," but they seem to have an important *rôle* in the division-process.

Let us suppose that a young egg-cell has sixteen chromosomes or idants, 16A ;
in the course of maturation the number is reduced by a half to 8A ;
the mature egg-cell is fertilised by a (reduced) spermatozoon with eight chromosomes, 8B ;
the fertilised egg-cell has then eight maternal and eight paternal chromosomes, 8A + 8B ;
the young germ-cell capable of initiating a new generation has the same ;
in the maturation of this young egg-cell reduction occurs to 4A + 4B ;
it is fertilised by a sperm of analogous history with 4C + 4D ;
the fertilised egg of the second generation has therefore 4A + 4B + 4C + 4D ;
similarly, the fertilised egg of the third generation may have 2A + 2B + 2C + 2D + 2E + 2F + 2G + 2H ;
similarly, in the fourth generation the chromosomes may be A + B + C + D + E + F + G + H + I + J + K + L + M + N + O + P (sixteen all different).

But the number of different chromosomes *need* not mount up so rapidly, for some of the paternal chromosomes may be the same as maternal. Moreover, the reducing division need not leave the maximum number of different chromosomes. The number sixteen, by hypothesis characteristic of the species, cannot be exceeded:

but the heterogeneity may spread into the individual chromosomes, affecting the ids.

Summary.—Put as simply as possible, the case is as follows.

The independently heritable and variable qualities of an organism are represented in the young germ-cell by a number of material elements (determinants).

As the young egg-cell ripens it divides in such a way that its determinants are reduced in number by one-half. Not that it need lose any particular kind of determinant, corresponding let us say to the colour of the eye or the colour of the hair, for each kind of determinant is represented in multiplicate. It loses one-half of its sets of determinants. The same happens with the ripening sperm-cell.

When the mature egg-cell is fertilised by the mature sperm-cell, the number of sets of determinants is once more raised to what it was in the young cells before maturation. But though the number of sets is the same as before, the collocation of the sets is not the same. At any rate, it need not be the same ; for there is an *apparently* random reduction.

The character of the offspring depends upon the adjustments arrived at among the different sets of determinants of maternal and paternal origin.

Hypothesis of Development.—Postulating an equipment of primary constituents or determinants within the germ-plasm, Weismann proceeded to elaborate a hypothesis as to the manner in which these determinants determine the cells or cell-groups to which they correspond.

The fertilised egg-cell divides and redivides, and at first the resulting cells (blastomeres) of the embryo are often equivalent to one another. This is demonstrable experimentally, for if the first four cells of the lancelet's ovum, for instance, be shaken apart, each goes on developing on its own account and forms a complete larva. In other cases, the resulting cells are heterogeneous from the first division onwards ; and, in any case, they soon become heterogeneous—that is to say, they form certain parts of the embryo, and these only. In other words, there must be a distribution of determinants in the course of segmentation.

But if the various kinds of determinants are to get into appropriate cell-groups, this cannot be a matter of chance. Therefore, we must further postulate that from the first each determinant has a definite position in relation to its neighbours, that the germ-plasm is not a mere loose aggregate of determinants, but that it possesses a structure, an architecture, in which the individual determinants have each their definite place. It must be borne in mind that the germ-cell is a unity, a potential organism, and not a heap of hereditary contributions. Weismann supposes that the determinants are kept in relation to one another by "vital affinities," by internal forces, some exhibition of which is, indeed, demonstrable, as when a chromosome or ribbon of ids splits into a double ribbon of ids.

But if the mechanism of the distribution of determinants is by cell-division—one of the features of which is that the chromosomes are halved with minutiose accuracy, so that each of the two daughter-cells obtains a longitudinal half of each chromosome—how does it come about that different determinants pass into different cells of the embryo? This difficulty led to the further hypothesis that, while ids may divide into two identical halves, they may also divide into two dissimilar halves. Weismann supposed that besides integral (*erbgleich*) division of the nucleus, there is also differential (*erbungleich*) division. The reality of this differential division—which many histologists vigorously dispute—cannot be directly demonstrated any more than the splitting up of a complex molecule into different molecules can be demonstrated. But in both cases we may infer the occurrence from the results. It is not a hypothesis, but a fact, that a cell may divide into two daughter-cells, one of which goes to form ectoderm, while the other goes to form endoderm, and this implies some sort of differential division. What internal forces or vital affinities are concerned we do not know.

If an egg-cell can divide differentially into a primordial ectoderm-cell and a primordial endoderm-cell, or into a formative

cell and a purely nutritive cell, and so on, it seems legitimate to suppose that corresponding differential divisions on a finer scale go on in the course of development. The embryonic cells go on dividing into daughter-cells having dissimilar developmental import or prospective value, and "such differential divisions will continue to occur until the determinant architecture of the ids is completely analysed or segregated out into its different kinds of determinants, so that each cell ultimately contains only one kind of determinant, the one by which its own particular character is determined. This character, of course, consists not merely in its morphological structure and chemical content, but also in its collective physiological capacity, including its power of division and duration of life" (1904, vol. i. p. 378).

It goes without saying that development also includes many integral divisions. Cells are continually producing their like, especially when there are numerous similar organs or parts in the organism. It must also be noted that the segregation-process cannot be pictured unless we suppose that the determinants—being alive—can multiply among themselves, so that a cell dominated by one kind of determinant may contain a whole army of determinants of that kind. We must also suppose that determinants may remain for a long period in an inactive state, and that it is only when they find themselves in an appropriate environment, largely determined by the cellular neighbourhood, that liberating stimuli awaken them to their controlling power.

The Breaking-up of the Determinants.—The segregation or distribution of the determinants goes on, and each unit-area or cell of the developing organism becomes the seat of a particular kind of determinant or of a contingent of these. What then happens? Weismann supposes that the determinant, having attained mature strength and its appropriate environment, breaks up into the biophors which compose it, and that these

migrate from the nucleus into the cell-substance. But there a struggle for food and space must ensue between the protoplasmic elements already present and the newcomers, and this gives rise to a more or less marked modification of the cell-structure. The biophors need not be supposed to correspond in advance to particular constituent parts of the cell, such as muscle elements or chlorophyll corpuscles; it is more plausible to suppose that they are the architects of these. Of course, they must have some definite character, but they need not be the infinitesimal rudiments of what they form. Many of them may be regulative, rather than formative. They may be organisers as well as architects. We need not stint their qualities, for they are *alive*.

Weismann does not conceive of the determinants as "seed-grains of the individual characters of the organism"; they are "codeterminants of the nature of the part which they influence." Like colonists entering upon a new territory, they owe their power to their co-operation. Again, the "character" of the cell—its size, intimate structure, length of life, and so forth, is not determined by a number of special determinants for each feature in the character. "There are only determinants of the whole physiological nature of the cell," and they work out the character of the cell in co-operation with one another and with the cell-body into which they have penetrated.

We cannot give a short account of the ingenious elaborations of the theory of determinants, by the aid of which Weismann has endeavoured to give a consistent all-round interpretation of special phenomena, such as budding, fission, regeneration of lost parts, alternation of generations, dimorphism, polymorphism, and so on. He supposes, for instance, that in those organisms which can multiply by liberating a bud or a fraction of the body there must be in many of the cells a residual contingent of determinants—amounting, it may be, to a representation of the entire germ-plasm—and that this contingent

remains latent until special circumstances arise which call it into activity.

Note on Regeneration.—When half of a highly differentiated Infusorian like *Stentor* regenerates the missing half, we suppose that it does so because in each half there are diffusely distributed "specific units" or "groups of determinants," which can in appropriate environment grow into wholes. We are encouraged to hold this hypothesis since we know that slices of *Stentor* a millimetre or less in thickness can re-grow wholes.

We shift the experiment to a slightly higher level, and we find that fragments of relatively simple multicellular animals, such as Hydra and Planarians, can grow into entire organisms. We suppose that the excised groups of cells have among them a sufficient complement of "specific units" to ensure the development of a complete organism.

But as we ascend higher in the scale, we find that while the earthworm can re-grow a new head or a new tail, a few median segments cut out of the middle of an earthworm will soon die. A crab can re-grow a lost limb, but the limb cannot re-grow a crab. The inference is that as differentiation increases the diffuse distribution of "complete specific units" ceases, so that the excised part is no longer a viable fragment. All this points to the reality of differential cell-division.

If the eye-bearing horn of a snail be cut off, it is regenerated over and over again, with the complex eye complete. If the eye of a crab be excised, there is usually regenerated an antenna instead of an eye, but if the optic ganglion is not injured a normal eye is regenerated. If the front of the eye of a newt or of a salamander be cut off, a new lens is regenerated. All this points to the hypothesis that within limits, probably punctuated by natural selection, the maimed stump or foundation of an important organ retains in reserve a contingent of units capable of growing the whole of that organ. Thus, while the distribution of complete residual specific units or ids becomes more and more

restricted, there is a much more useful retention, at spots liable to injury, of local contingents of "organ-forming units" which can replace lost parts.

Difficulties.—1. If definite determinants are distributed in development as the number of unit-areas or cells increases, how is it that an isolated group of cells, cut off from a begonia-leaf, a potato-tuber, a hydra-polyp, a sea-anemone, a simple worm, may in appropriate conditions grow into an entire organism? It must be noted, in the first place, that this capacity is more or less restricted to relatively simple organisms. In the second place, the theoretical answer is that in such cases the cells retain a representation of the whole germ-plasm in an inactive state, though each one of them is differentiated under the control of a particular set of determinants.

2. A man has a peculiar "crooked nose" and his son has the like. Are we to suppose that the inheritance includes "crooked nose"-determinants? Weismann would say "emphatically not." A large number of different kinds of determinants are concerned in the up-building of the nose, and they work co-operatively towards a general result. There may be some slight peculiarity in those that contribute, let us say, to the cartilage of the nose, and this peculiarity may, in the course of the co-operative development, lead to a crooked nose as the result of some inequality of pressure during the early formative period. The results of experimental embryology show clearly that the behaviour of particular cells in development is not absolutely stereotyped; they will do their best, as it were, to work out a constant result, but if this is interfered with environmentally they will do something else. At the same time, it is very interesting that abnormal larvæ—*e.g.* the so-called Lithium-larvæ of sea-urchins—have a remarkable power of righting themselves when they are relieved from the disturbing influence of the abnormal environment.

Objections to the Theory of Determinants.—Some biologists

have objected to Weismann's theory of determinants, because, as they say, no one has ever seen or can ever hope to see one. Determinants are scientific fictions and all discussion of them is in the air. But the same sort of objection may be raised against the theory of, let us say, the ether. The point is whether the concept of determinants helps us to interpret visible phenomena. Science works from beginning to end with imaginative concepts which facilitate description and formulation, and which are so truly representative of the invisible that we can utilise them in prediction.

Other biologists, who are aware of the impossibility of a science without imaginative concepts, object to the theory of determinants on the ground that they can be done without. Thus Prof. Yves Delage rejects all determinants, primary constituents, or *particules représentatives*, and will only postulate a germ-plasm with "an extraordinarily delicate and precise physico-chemical composition." "There are not," he says, "in the germinative plasm any distinctive particles representing the parts of the body or the characters and properties of the organism" (1903, p. 749). What is there, then? According to Delage, the germ-cell contains a number of characteristic chemical substances—which every one admits—characteristic of the chief categories of cells; and its development is comparable to the flow of a river, now running deep and again shallow, here forming a waterfall and there an eddy, but always explicable in terms of action and reaction between the flowing water and its surroundings. Given the power of developing (which no one understands), given a characteristic chemical composition (which every one admits), and given an appropriate environment (which nobody can deny), and *voilà tout*. There is no more need to cumber biology with determinants and biophors than there was to cumber astronomy with Ptolemaic circles and epicycles.

But even in the apparently simplest cases it seems impossible

to dispense with the concept of "units," or "primary constituents" or "determinants" or groups of these including all the specific characters. Take the case of the common Infusorian *Stentor*. It seems to be certain that a thin slice, a millimetre thick, of this unicellular organism may, in appropriate conditions, grow into a complete individual, with vibratile oral cilia, smaller superficial cilia, a mouth, a long necklace-like nucleus, three smaller nuclei, a contractile vacuole, internal contractile fibrils, and so on. Is it possible to think of this marvellous regeneration of a highly differentiated unity from a thin slice, without postulating "units" of some sort, which, when removed from the system as a whole, have yet the power of reconstituting that system? (See Weldon, 1905, p. 42.) Similarly, a thin slice of the multicellular Hydra-polyp may, in appropriate conditions, grow into an entire and complete Hydra. Is it possible to conceive of this apart from the postulate of diffusely distributed "specific units"?

Prof. H. E. Ziegler has briefly and temperately stated the two most frequent objections to the theory of representative particles.

1. When we try to interpret any result or occurrence we must refer it to what is known. If we interpret it in terms of a something invented for the purpose we are simply making a fictitious hypothesis. When we refer facts of inheritance to observable processes—*e.g.* in the chromosomes of the nuclei—we are making scientific progress; but when we deduce the phenomena of inheritance from the behaviour of pangens or determinants which have been invented we are simply indulging in verbal speculation. As it appears to us, this is not a just statement of scientific procedure. The imaginary pangens or determinants are elements in a notation like the graphic symbols of chemical molecules: their utility does not depend on any visible reality; their validity is tested by the degree in which they enable us to formulate conceptually what does occur, and

to reach forward from this formulation to more precise observation and experiment. It goes without saying that the moment the symbolic notation is shown to be inconsistent with demonstrable facts, it must be thrown overboard and replaced by another.

2. It is difficult, Ziegler says, to think out clearly what we mean by a unit-character and by its being represented by a unit-germinal-constituent, whether pangen or determinant. Many a quite definite character of an organism depends upon a multitude of growth-conditions, and to conceive of the character being represented in the germ by one representative particle is as difficult as it is to conceive of an infinite number of representative particles, one for each item in the character.

But it should be noted that Weismann simply assumes as many determinants in the germ-plasm as there are parts in the organism capable of independent and transmissible variation. The fiddling string and bow on a grasshopper's thigh and wing will have at least one determinant each, but one determinant may suffice for all the millions of red blood corpuscles in man. Again, Weismann expressly emphasises his view that "determinants are not seed-grains of individual characters, but co-determinants of the nature of the parts which they influence. There are not special determinants of the size of a cell, others of its specific histological differentiation, and still others of its duration of life, power of multiplication, and so on; there are only determinants of the whole physiological nature of a cell, on which all these and many other 'characters' depend." Or again, "There are no determinants of 'characters,' but only of parts. The germ-plasm no more contains determinants of a 'crooked nose' than it does those of a butterfly's tailed wing; but it contains a number of determinants which so control the whole cell-group in all its successive stages, leading on to the development of the nose, that ultimately the crooked nose must result, just as the butterfly's wing, with all its veins, mem-

branes, tracheæ, glandular cells, scales, pigment deposits, and pointed tail, arises through the successive interposition of numerous determinants in the course of cell-multiplication."

In any case, whether the idea of representative primary constituents commends itself to us or not, we must remember that it is a *fact* that the organism—unified as it is—is built up of a very large number of independently variable, independently heritable items.

The Persistence of the Germ-plasm.—We have given an outline of the consistently-thought-out scheme which Weismann has suggested as an interpretation of development—the distribution of the determinants, their "maturation," their "liberation," their migration from the nucleus, their dissolution into biophors, and the manner in which the biophors may control the area or cell in which they find themselves. But it remains to inquire how the germ-cells which start the next generation are constituted. If the building-up of the body involves segregation of the determinant architecture into smaller and smaller groups, how does the organism produce germ-cells—that is, cells with intact germ-plasm—with a complete equipment of determinants? The answer, already given in Chapter II., is that it does not in the strict sense produce them; *they are there all the time.*

In more detail, Weismann's answer (1885)—*the theory of the continuity of the germ-plasm*—is that in the divisions of the ovum the whole of the germ-plasm is not broken up into determinant groups; part of it is kept intact and handed on from cell to cell along a lineage or "germ-track," which may be very short or very long, until, sooner or later, it stamps a cell as a primordial germ-cell. In other words, while most of the cells, derived by division from the fertilised ovum become differentiated as body-cells, some of the cells retain a quota of intact germ-plasm, and eventually give rise to recognisable germ-cells. Body-cells and reproductive cells alike owe their being to the

germ-plasm of the fertilised ovum, and are its lineal descendants; but the somatic cells are dominated by particular segregated and liberated sets of determinants, whereas the germ-cells are those, or the descendants of those, that retain the complete equipment.

In studying the development of the threadworm of the horse (*Ascaris megalocephala*), Boveri found that the two first segmentation-cells both receive the four chromosomes characteristic of the species; one gives rise to all the body-cells, the other to all the germ-cells. In the lineage of the former there is a visible reduction of the chromatin; in the lineage of the other there is no such reduction. This is perhaps the clearest of all cases, and the case of some of the Diptera is almost as clear. But theoretically it makes no difference how long the "germ-track" may be, or how long it may be before recognisable germ-cells are seen in the developing organism. In some familiar cases—the alternation of generations in Hydroids—the reproductive cells, as such, are not demonstrable till after the asexual generation forms a sexual bud; and yet, even here, we know some very interesting facts regarding the germ-cell lineage.

§ 3. *Note on Rival Theories*

Darwin's Theory of Gemmules.—Darwin's provisional theory of pangenesis suggests, as we have already seen, that particular cells of the body give off representative gemmules, and that these are collected in the reproductive cells. When the fertilised egg-cell divides and redivides, the army of gemmules is contained in each cell; but at every stage of development particular kinds of gemmules are stimulated to activity, and proceed to influence the area in which they find themselves—an area corresponding to that from which they were originally given off. As Weismann points out, this hypothesis requires us to postulate an enormous number of specific stimuli, distributed through the crowd of

embryonic cells, which almost amounts to assuming the differentiation which the theory was intended to interpret.

Weismann tries to avoid this difficulty by assuming an autonomic dissolution of the determinant complexes, though he does not reject the view that the differently related vital areas or cells in which the determinants find themselves may serve as liberating stimuli. In a marching army the differently related localities serve as liberating stimuli to the diverse kinds of men composing the army; here the sappers and miners go to work, there the commissariat erects a depot, in a third place a heliograph is set up, and so on.

Herbert Spencer's Theory of Physiological Units.—Spencer postulated "physiological units," ultimate life-bearing elements, intermediate between the chemical molecules and the cell. Just as the same kinds and even the same number of atoms may compose, by different arrangements, numerous quite different chemical molecules—*e.g.* in the protein-group—so out of similar molecules diversely grouped an immense variety of "physiological units" may be evolved, like the variety of patterns in a kaleidoscope. But for each kind of living creature Spencer postulated "physiological units" or "constitutional units" of one kind.

Spencer credited his "constitutional units" with much.

1. They carry within them the traits of the species, and even some of the traits of the ancestors of the species; the traits of the parents, and even some of the traits of their immediate ancestors; and the inborn idiosyncrasies of the individual organism itself.

2. They "must be at once in some respects fixed and in other respects plastic; while their fundamental traits, expressing the structure of the type, must be unchangeable, their superficial traits must admit of modification without much difficulty; and the modified traits, expressing variations in the parents and immediate ancestors, though unstable, must be considered as capable of becoming stable in course of time."

3. Moreover, "We have to think of these physiological units

(or constitutional units, as I would now rename them) as having such natures that while a minute modification, representing some small change of local structure, is inoperative on the proclivities of the units throughout the rest of the system, it becomes operative in the units which fall into the locality where that change occurs."

4. Furthermore, Spencer supposed "an unceasing circulation of protoplasm throughout an organism," such that "in the course of days, weeks, months, years, each portion of protoplasm visits every part of the body"—a wild assumption. Therefore, "we must conceive that the complex forces of which each constitutional unit is the centre, and by which it acts on other units while it is acted on by them, tend continually to remould each unit into congruity with the structures around; superposing on it modifications answering to the modifications which have risen in these structures. Whence is to be drawn the corollary that in the course of time all the circulating units—physiological, or constitutional, if we prefer so to call them—visit all parts of the organism; are severally bearers of traits expressing local modifications; and that these units, which are eventually gathered into sperm-cells and germ-[egg-]cells, also bear those superposed traits."

5. According to Spencer, "sperm-cells and germ-[egg-]cells are essentially nothing more than vehicles in which are contained small groups of physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to"; and "if the likeness of offspring to parents is thus determined, it becomes manifest, *a priori*, that, besides the transmission of generic and specific peculiarities, there will be a transmission of those individual peculiarities which, arising without assignable causes, are classed as spontaneous."

We have illustrated Spencer's position at some length because so many British biologists have recoiled from what they call the complexity of Weismann's theory. But a little consideration will show that the protagonist of British biology invented a system in comparison to which Weismann's is simplicity.

Nor can we close our exposition without recalling how Spencer confessed that "the actual organising process transcends conception. . . . It is not enough to say that we cannot know it;

we must say that we cannot even conceive it. . . . If even the ordinary manifestations of the dynamic element in life which a living body yields from moment to moment are at bottom incomprehensible, then still more incomprehensible must be that astonishing manifestation of it which we have in the initiation and unfolding of a new organism. . . . Thus, all we can do is to find some way of symbolising the process so as to enable us most conveniently to generalise its phenomena; and the only reason for adopting the hypothesis is that it best serves this purpose."

But Spencer's hypothesis only serves the purpose because the constitutional units are gradually invested with the powers of effective response, co-ordination, and the like which remain the secret of the organism as a whole—the secret of life, which many think will never be read until we recognise that it is also the secret of mind.

De Vries's Theory of Intracellular Pangenesis.—A theory different from Darwin's and also from Weismann's has been suggested by Hugo De Vries under the title "Intracellular Pangenesis." The gist of it may be summed up as follows:

1. Organisms are built up of unit-characters, independently variable and independently heritable.

2. These unit-characters are represented *in potentia* in the hereditary substance of the nucleus of the germ-cell by definite bodies (pangens), far too minute to be visible, but together constituting the chromosomes of the nucleus.

3. The pangens multiply in the idioplasm of the nucleus, and some of them migrate into the surrounding cytoplasm, where they become active, dominating it, and giving it a particular character. But a representative contingent of pangens always remains in the nucleus and is handed on from cell to cell by nuclear division. Into each cell as it is formed a fresh migration of pangens occurs.

Other Suggestions.—It need hardly be said that many other

schemes have been suggested with the laudable end of throwing some light on one of the most familiar facts of life—the development of the germ. Thus the illustrious physiologist of Prague, Ewald Hering, and that acute English thinker, Samuel Butler, have suggested that development is, as it were, a materialised recollection of the past; Ernst Haeckel conceived of development as due to the persistence of characteristic and complicated wave-motions acquired in the past by the organic molecules; many others have looked at the matter chemically, "the same substances and mixtures of substances being reproduced in similar quantity and quality with regular periodicity."

A scholarly account of these and other suggestions will be found in Delage's great work on heredity, where every known view is presented with fairness and lucidity and criticised with unrivalled acuteness and justice. There also will be found the finest exposition of the view, which we find ourselves quite unable to entertain, that it is possible to dispense with any postulate of "representative particles."

§ 4. *Weismann's Theory of Germinal Selection*

In 1895–6 Weismann expounded an ingenious hypothesis, the main idea of which is expressed in the phrase "Germinal Selection." It is an extension of the biological concept of "struggle" to the individual items which compose the germ-plasm—*i.e.* the inheritance.

Extension of the Struggle-and-Selection Formula.—In human affairs there is often struggle between different societary forms—as in war and international commercial competition; and no one doubts that this involves a process of selection. This is often so complex that it must be termed superorganic. An adumbration of it is seen in the wars of the ants, and in the competition between a pack of carnivores and a herd of herbivores. Similarly, within one human societary form there may be

struggle between rival organisations and rival institutions, and no one doubts the reality of an intrasocietary selection. This, again, is more complex than the ordinary personal or individual selection.

"Personal" Selection.—Of personal or individual struggle there are many forms and phases, notably (*a*) the competition between fellows of the same kin for food and foothold, which is not self-regarding only, but for the sake of mates and family as well; (*b*) the opposition between foes of quite different kin—*e.g.* between birds of prey and small mammals; and (*c*) the struggle between organisms and the changeful inanimate environment. Besides these three main forms there are many special cases, such as the battles between males of the same species for the possession of females, as in the case of seals and stags, and the sometimes serious disagreements between mates, so quaintly illustrated in some spiders. Corresponding to these different forms of struggle there are different modes of selection and elimination.

Intra-organismal Selection.—In 1881 Roux introduced the idea of a *struggle of parts within the organism.* He pointed out that functional stimulus tends to strengthen an organ, that there is a "quantitative self-regulation of an organ according to the strength of the stimulus supplied to it." It may be over-compensated for its expenses, and grow, just as the opposite conditions may lead to atrophy. It is well known that if all the work of renal excretion be thrown on *one* kidney, that organ increases greatly in size, and that if the nerve to a muscle or gland be cut, that muscle or gland begins to degenerate. If we pursue this line of thought we begin to realise what is meant by a struggle of parts within the organism, and by intra-organismal selection. Some change occurs in the conditions of nutritive and other stimuli; there are limitations affecting the nutritive supply, the amount of available space, and so on; and there has to be an internal give and take, a mutual re-

adjustment of parts—in fact, a struggle. This is often referred to as intra-selection or histonal—*i.e.* tissue—selection.

As Weismann says, "The tissues and the parts of the tissues have to distribute and arrange themselves so that each comes to fill the place in which it is most effectively and frequently affected by its specific stimulus—that is, the stimulus in regard to which it is superior to other parts; but these places are also those the occupation of which by the best reacting parts makes the whole tissue capable of more effective function, and therefore makes its structure the fittest. . . . The cells which assimilate more rapidly because of the more frequent functional stimulus increase more rapidly, draw away nourishment from the more slowly multiplying cells around them, and thus crowd these out to a greater or less extent" (1904, vol. i. p. 247).

As Weismann points out, it is impossible at present to give any precise limitation of the respective spheres of personal and histonal selection. The intra-organismal struggle may be, so to speak, the internal adjustment necessary towards a result which the external process of personal selection is bringing about. "The differentiation of the particular kinds of cells is an ancient inheritance, and depends upon personal selection; but their distribution and arrangement into specially adapted tissues, so far as there is any plasticity at all, depend upon histonal selection." The architecture of every organ is implicit in the germ and must be referred to a long-drawn-out process of personal selection, but the particular *local* modifications of the architecture may be adjusted by the intra-organismal struggle. And, again, it must be borne in mind that personal selection may put a full stop at any moment to the achievements of histonal selection if they affect the viability of the creature as a whole. A hypertrophied organ may express the organism's internal endeavour to make the best of a new situation, but it may be fatal.

In so far as a process of intra-organismal struggle is of *normal*

occurrence in development, where we often see one organ waxing and another waning, we must regard it as part of the plan of campaign which is hereditarily predetermined in the germ-plasm. But since the organism develops in intimate dependence on a changeful environment, we are prepared for local modifications of adjustment arising as the results of histonal selection. Many malformations represent attempts on the organism's part to solve an insoluble problem forced upon it by peculiar environmental conditions; many individual adaptations are wrought out by the *modus operandi* of histonal selection in the individual lifetime, and are of real value to the organism that acquires them. But there is no good reason for believing that either can be entailed on the offspring.

None the less, it is important that the student of inheritance should vividly realise the existence of this *modus operandi* which Roux called the "struggle of parts within the organism." For, although we cannot say that it has any direct evolutionary importance in securing new steps in evolution, and although we do not understand how it is that parts regulate themselves appropriately in reference to new conditions of stimulus—for that is obviously part of the secret of life itself—it is useful to bear in mind that there is in a real sense a competition among organs, a struggle of parts, and a warfare among cells. Vivid illustrations may be found in the histolysis or disruption of tissue associated with metamorphosis (*e.g.* in many insects), in the behaviour of teratogenic growths, in the involutions or degenerations associated with senility (*e.g.* in the invasion of the brain of the aged parrot by hungry "neurophagous" cells), and in the familiar fact that the hypertrophy of one organ may handicap or even suppress another organ.

In short, the concepts of struggle and selection may be extended to the parts of the organism.

Struggle between Gametes.—There may be struggle between groups of organisms, struggle between individual organ-

isms, struggle between organisms and their surroundings, and struggle between parts within the organism—between organs, tissues, and cells. Can the formula be extended further?

Before we pass to Weismann's proposal to extend the concept "struggle" to the determinants within the germ, it may be of interest to call attention to a form of struggle and selection which may be interpolated between Roux's histonal selection and Weismann's germinal selection. Although Weismann does not seem to favour the idea, it seems to us that there is a real and important struggle between the germ-cells as such.

1. There is a well-known struggle between potential ova. In many cases the majority are sacrificed to a minority, which sometimes literally feed upon their fellows. In the common freshwater polyp, *Hydra*, and in a common marine polyp, *Tubularia*, only one egg-cell usually survives out of an originally numerous sisterhood, reminding one of the combat to the death which may occur among sister queens in a beehive.

2. There is a kind of struggle between the hundreds of spermatozoa in their race towards the ovum, which only one of them in normal conditions will fertilise. In the familiar fertilisation of frog's ova, several spermatozoa may be seen boring their way through the jelly surrounding the ovum; but after one has entered the ovum a rapid change in the peripheral protoplasm seems to shut the door on others. It may well be, allowing a margin for the purely fortuitous, that the most vigorous, most sensitive spermatozoa tend to fulfil their particular office of fertilising the ova, and *this will tend to be to the advantage of the species*. Again, we are quaintly reminded of the race between the drone-bees to overtake the queen in her nuptial flight. Usually, one drone effects sexual union, and all the rest are futile.

3. There is sometimes, according to Iwanzoff and others, a struggle between ova and spermatozoa, for young ova may literally *digest* intruding sperms. There is also a form of selection

involved in the fact that in some cases there are more ova than sperms, though the reverse is usually the case. Thus Maupas has shown that in *Rhabditis* and some other threadworms only about a third of the ova *can* be fertilised; there are no sperms left for the other two-thirds produced later.

Many other illustrations might be given, but our point here is simply this, that a vivid realisation of the visible struggle among germ-cells or gametes, and the frequently discriminate nature of the ensuing elimination, may lead us naturally to an appreciation of germinal selection which deals with the wholly invisible.

Statement of Weismann's Theory.—As we have seen, Weismann pictures the germ-plasm as composed of *an army of living determinants*—that is to say, of an aggregate of primary constituents (or potentialities), of particular parts of the organism. These particular parts will not arise if their determinants are absent from the germ-plasm, and we *know* in some cases—*e.g.* in the development of some Ctenophores (usually globular free-swimming Cœlenterates)—that the abstraction of certain cells from the embryo means an absence of certain structures from the adult.

Let us suppose, then, that the physical basis of inheritance is composed of a multitude of representative vital particles, which have the capacity of feeding, growing, and multiplying. As the supply of nutriment necessarily fluctuates continually in the reproductive organs as a whole, "we may therefore assume that there are similar irregularities and differences in the minute and unobservable conditions of the germ-plasm likewise, and the result must be a slight shifting of the position of equilibrium as regards size and strength in the determinant system; for the less well-nourished determinants will grow more slowly, will fail to attain to the size and strength of their neighbours, and will multiply more slowly" (1904, vol. ii. p. 117).

Every one must admit that there are fluctuations in the nutritive supply of the germ-cells, and to these, according to

Weismann, we must refer those individual germinal variations which form part of the raw material of evolution. But it can hardly be imagined that all the determinants or hereditary constituents are equally vigorous, or have equal assimilating power. Thus, a determinant may become weaker because there is less food for it, and also because it has less power of utilising the available food. If a determinant is thus weakened, its determinate—the structure to which it corresponds—will also be weakened; and we call this a germinal variation on the down-grade. On the other hand, a vigorous determinant with strong assimilative power will tend to become stronger if it is well and appropriately fed. Its determinate will be correspondingly strengthened, and we call this a germinal variation on the up-grade.

"To the ascending progression there are limits set, not only by the amount of food which can circulate through the whole id (a complete system of determinants), but also by the neighbour determinants, which will sooner or later resist the withdrawal of nourishment from them; but for the descending progression there are no limits except total disappearance, and this is actually reached in cases in which the determinants are related to a part which has become useless" (Weismann, 1904, vol. ii. p. 118).

"If the germ-plasm be a system of determinants, then the same laws of struggle for existence in regard to food and multiplication must hold sway among its parts that obtain between all systems of vital units—among the biophors which form the protoplasm of the cell-body, among the cells of a tissue, among the tissues of an organ, among the organs themselves, as well as among the individuals of a species and between species which compete with one another."

When a structure becomes useless in the life of a species, those individuals who have more of it are no better off than those who have less of it; natural selection no longer operates

as far as that structure is concerned; a state of panmixia, as it is called, sets in; and the structure in question tends to dwindle. But this external selection is abetted by the germinal selection, for when a determinant corresponding to the useless structure becomes weaker through the intragerminal fluctuations of nutrition, "it finds itself upon an inclined plane, along which it glides very slowly but steadily downwards. The determinant whose assimilative power is weakened by ever so little is continually being robbed by its neighbours of a part of the nourishment which flows towards it, and must consequently become further weakened." By hypothesis, personal selection cannot help it to persist—*i.e.* cannot favour those individuals in whose inheritance it is relatively stronger; therefore, by an internal struggle and selection, which may be quite real though quite unverifiable, the determinants of a disused part dwindle away in the course of many generations. On the other hand, when personal selection favours the increase of a part—*i.e.* favours individuals whose inheritance includes strong determinants of that part, again the internal struggle will back up the external sifting. In short, nothing succeeds like success.

The theory helps us to understand the slow dwindling of useless structures, but it is also applicable to the augmentation of useful parts. Suppose it be important for humming-birds to have a longer tongue, and that natural selection favours variants with longer tongues. Corresponding to the tongue there are, by hypothesis, in the germ-plasm, several sets of homologous determinants. (We need not complicate the argument by recognising that many different kinds of determinants will be required for a complex structure like the tongue.) There are fluctuations in the food-supply and some tongue-determinants get the advantage; they become stronger, they exhibit a plus variation, and as they become stronger they increase in assimilative capacity. They therefore tend to predominate more and more over other tongue-determinants which

may exhibit a minus variation; and personal selection favouring the birds with longer tongues—*i.e.* birds in whose inheritance there is a predominance of tongue-determinants varying in the plus direction—the direction of variation will remain positive. In the case of artificial selection the continuance in the plus direction may go much further and much more rapidly than in the case of natural selection, for rapid increase of any part is apt to prejudice the viability of the whole organism, which in the case of domesticated animals is artificially preserved. Thus we have the Japanese breed of cocks with feathers six feet long.

Illustration.—It is admitted by all that in the course of evolution the hind-limbs of whales have dwindled away and are now represented simply by vestigial structures. As the far-back ancestors of the whales of to-day became thoroughly aquatic and took to swimming with great strokes of the tail, the hind-limbs became functionless, futile, and actually in the way. Natural selection would favour those individuals whose hind-limbs varied in a retrogressive or minus direction; that is to say, natural selection would favour those individuals in whose germ-plasm or inheritance determinants of the hind-limb varying in a minus direction came to be predominant over those varying in a plus direction. As the result of persistent personal selection the determinants varying in a minus direction would come to be more and more dominant. Weismann's point is, that when a bias in favour of minus determinants or short hind-limb determinants was thus established, it would go on increasing automatically because of germinal selection. Determinants varying in a plus direction, in the direction of longer hind-limbs, would be more and more thoroughly vanquished in the germinal struggle with the more numerous, more vigorous, perhaps larger determinants varying in the direction of utility. And after personal selection had ceased to operate —*e.g.* when the hind-limbs had quite sunk beneath the surface—

the germinal selection would still continue, and thus we can picture to ourselves a *modus operandi* whereby the useless organ would dwindle more and more.

Similarly, every one admits that the huge canines of various mammals have evolved from relatively small teeth in the same position. For many generations natural selection would favour variants with larger canines—*i.e.* those in whose germ-plasm or inheritance canine-determinants varying in the direction of greater size and strength of teeth were predominant. "The moment that these come to predominate in the germ-plasm of the species, at once the tendency must arise for them to vary *still more strongly* in the plus direction, not solely because the zero-point has been pushed further upwards, but because they themselves now oppose a relatively more powerful front to their neighbours—that is, actively absorb more nutriment, and upon the whole increase in vigour and produce more robust descendants. From the relative vigour or dynamic status of the particles of the germ-plasm an ascending line of variation will thus spontaneously arise, precisely as the facts of evolution require." Furthermore, if we admit this consideration we can in some measure understand why the ascending line of variation often tends to go too far; and sometimes does go too far when the check of natural selection is removed by the artificial conditions of domestication.

Value of the Theory.—Weismann emphasises the following, among other advantages of the theory of germinal selection. It suggests an interior mechanism which interprets the occurrence of definitely directed variations, the occurrence of appropriately useful variations at the right place and time, the diminution of organs below the level touched by personal selection or its cessation (panmixia), the occasional exaggeration of organs beyond the limits of demonstrable utility, the simultaneous occurrence of many similar variations, and so on.

It must remain a question for personal judgment whether

these and other alleged advantages of the theory are real advantages. Does the theory clarify our conception of inheritance? and does it suggest experimental work, on which, after all, we must base our conclusions as to these abstruse questions? Do the advantages of the theory outweigh the difficulties?

The chief difficulties are (1) in the argument that the struggle will work out in a *discriminate selection*, and (2) in the postulate that a slight advantage gained by a set of determinants will be able to persist through a long series of cell-divisions, till the sex-cells of the offspring are again matured.

Objections.—What we have stated above is not more than an outline of a theory which Weismann has developed with great subtlety and in great detail, and many objections may occur to our statement of the theory which are well met in the author's own presentation.

1. It has been objected that the whole concept of germinal selection is visionary and unverifiable. The point, however, is: does this hypothetical construction enable us to interpret the facts better? does it harmonise with visible facts? is it consistent with what we know of the behaviour of observable living units? It seems to us that an affirmative answer may be given. The concept deals with an invisible world, but it helps us to interpret such facts as the dwindling of useless parts, the excessive growth of more or less indifferent structures (such as some of the ornaments of shells), and in general the frequent definiteness of variation.

2. It may be objected that we can hardly think of invisible bodies such as determinants struggling for food. But why not? Size seems an irrelevant consideration. Cells which are invisible to the naked eye are seen under the microscope struggling for food. The germ-cells in the ovary of Hydra devour one another just as really as the embryos of the dog-whelk in their egg-capsules on the sea-shore, just as really as the locusts

in a swarm. And if there is competition among cells for food, why not among the chromosomes within the cell, and why not among the determinants within the chromosome?

Yet, is not the supply of food brought by the vascular fluids of the body always more than sufficient? Who can tell? When we consider, for instance, the enormous ovary of a cod—the familiar cod-roe of the breakfast-table—and its legions of eggs, can we be sure that the food-supply is always superabundant? Moreover, it is very improbable that all the hungry units are equally well-placed; how much more is there likely to be inequality within the labyrinth of the ovum-nucleus, which is a little world in itself? And again, it by no means follows that all the food supplied is appropriate, or that all the homologous determinants are equally able to use it.

As Weismann says, to suppose that food is always superabundant "seems to me much the same as if an inhabitant of the moon, looking at this earth through an excellent telescope and clearly descrying the city of Berlin, with its thronging crowds and its railways, bringing in the necessaries of life from every side, should conclude from this abundant provision that the greatest superfluity prevailed within the town, and that every one of its inhabitants had as much to live upon as he could possibly require" (1904, vol. ii. p. 156).

As an instance of severe criticism by an expert who sees no utility in these imaginative interpretations, we may quote the following passage from Prof. T. H. Morgan's *Evolution and Adaptation* (1903, p. 165): "Weismann has piled up one hypothesis on another as though he could save the integrity of the theory of natural selection by adding new speculative matter to it. The most unfortunate feature is that the new speculation is skilfully removed from the field of verification, and invisible germs, whose sole functions are those which Weismann's imagination bestows on them, are brought forward as though they could supply the deficiencies of Darwin's theory. This is,

indeed, the old method of the philosophisers of nature. . . . The worst feature of the situation is not so much that Weismann has advanced new hypotheses unsupported by experimental evidence, but that the speculation is of such a kind that it is, from its very nature, unverifiable, and therefore useless."

These are hard words, but it would have been more to the point to inquire whether Weismann's imaginative picture of what may go on within the microcosm of the germ-plasm is in any way contradictory of known biological results. Of course, the theory is "unsupported by experimental evidence," and "removed from the field of verification"; but why it is therefore "useless" we fail to see. It appears to us quite on the same plane as many symbolic interpretations in chemistry and physics, where we say that if we picture atoms and molecules, electrons and corpuscles, in such and such a way, then we can redescribe more clearly the observable sequences of conditions and results, and devise further experiments which will test the adequacy of our symbols and enable us to improve them. The struggle of determinants may not be quite as Weismann supposes, but the idea is a logical extension of the selective process which occurs at many different levels; it clarifies our picture of observable facts, and it stimulates further inquiry.

Summary.—Convinced that the theory of natural selection in the Darwinian sense required some rehabilitation, dissatisfied with the assumption of merely "accidental" variations, confronted with evidence of definitely directed variations, Weismann devised this theory of germinal selection. The personal selection of the possessors of a plus or minus variation in any part means, of course, that those organisms are favoured in which the corresponding determinants within the germ-plasm are varying in a plus or minus direction. But if there be inequality (in size and assimilating power) among the homologous determinants, and if there be fluctuations in the nutritive supply, there may come about a germinal struggle among the homologous deter-

minants. Those that are weaker will tend to become weaker still, those that are stronger will tend to become stronger still, and thus germinal selection fosters and strengthens personal selection. In other words, there is an internal reason for progressive variation (either plus or minus) in the direction of utility.

A Suggestion.—If we admit the concept of representative particles in the germ-plasm, which it seems to us is almost demanded by the facts of particulate inheritance, by the independent variability and heritability of often trivial peculiarities; and if we admit the probability of some sort of germinal struggle among these living units, which seems to us warranted by what we know of the behaviour of visible living units and by general biological considerations—then it seems at least interesting to ask whether we need limit the conception of germinal struggle to a competition between *homologous* determinants, as Weismann always does.

In personal selection, as we have seen, there are three distinct types of struggle—classified according to the parties involved—(*a*) between kindred or homologous organisms, (*b*) between organisms which are not akin, and (*c*) between organisms and the inanimate environment. Logically, we may look for the same three modes of struggle in the course of germinal selection. They might be illustrated (*a*) by struggle between, say, the maternal and the paternal, or the parental and the grandparental, homologous determinants of a single determinate; (*b*) by struggle between determinants of quite different kinds—*e.g.* between determinants of the notochord and the determinants of its more effective substitute, the backbone; and (*c*) by struggle between all or any of the determinants and a disturbing external influence, such as some toxin in the parent's blood or lymph, or some change in the osmotic conditions of the sea-water. Is there any theoretical reason why we should restrict the concept of germinal struggle, as Weismann does,

to competition between homologous determinants in relation to the fluctuating food-supply?

Testing the Theory.—The chief objections that have been brought against the theory of germinal selection are,—(1) that it is bound up with a particular notation and theory of development and evolution—in terms of representative particles or primary constituents, the determinants, which many regard as at once unverifiable and gratuitous; (2) that it cannot be objectively verified or directly tested by experiment, being, like many other scientific theories, part of an intellectual game with invisible counters; and (3) that it is gratuitous, since the results of evolution can be interpreted without this extension of the selection-process into the invisible microcosm of the germ-plasm. In answer to these objections, Weismann's original essays and later lectures on germinal selection seem to us quite sufficient, and we must ask the interested reader to consult the original documents and not to base his verdict upon a necessarily brief and incomplete presentation of the case. We offer this commonplace advice because some objectors raise difficulties which a perusal of the original documents would have shown to be inept.

The progressive course seems to be to take a set of facts from different fields, and to see whether the key which Weismann has given us does or does not fit. We propose, therefore, to assume the concept of a germinal struggle between primary constituents (not necessarily *homologous* determinants), and to inquire whether Weismann's suggestion has interpretative value.

1. No one is very willing to predict the hereditary result of pairing two organisms. Average predictions may be ventured in regard to the issue of a hundred or a thousand pairings. These predictions may be Galtonian or Mendelian, and they may be justified *on the average.* But individual results continually crop up which are unpredictable; and even apart from these valuable

generalisations—Galtonian and Mendelian—we are accustomed, in predicting the issue of crossings, to say that the offspring will exhibit a blended, or exclusive, or particulate expression of the parental characters. How often, however, must we not frankly admit, the individual result seems anomalous! Now, is not this result just what we should expect if germinal struggle is a reality?

2. No phenomenon of inheritance is more familiar than that of preponderant and exclusive inheritance, where, in regard to the expression or development of a given character, the offspring follows one parent preponderantly or exclusively, instead of being merely a "blend." If we suppose that ovum and spermatozoon have each a complete organisation of hereditary qualities (as we seem bound to suppose), and that the fertilised ovum has determinants representing the character in question from both parents and from the ancestors of both parents, may we not consistently interpret the hereditary re-expression of only one set, by supposing that there is a struggle for expression between the various sets—a struggle in which the most vigorous have for the time the mastery?

3. A frequent phenomenon of inheritance is a change in the direction of preponderance in the successive children of a large family. Suppose a virile middle-aged father and a much younger mother: the older children may be markedly paternal in the expression of their inheritance, the younger children as markedly of the maternal type. Introduce the conception of germinal struggle; suppose it to occur not only in the germ-cell lineage within the gonads, but in the fertilisation and afterwards; recall the fact that the ova tend to be more stable than the spermatozoa, being formed and to some extent fixed in very early days, whereas the spermatozoa continue to appear in crop after crop. At first we picture a victory on the part of the determinants of the relatively prepotent father; but gradually, in his post-mature spermatogenesis, there is a weakening of paternal determinants such that, in fertilisation, those from the mother have now a better chance of asserting themselves. Naturally enough, the Benjamin is after the mother's image and after the father's own heart.

4. A very young pigeon of hooded or frilled breed is mated with an old one: the first young are smooth-headed and smooth-breasted, but those of later broods have the specialised characteristics of the parents. May this not mean that in the too-young egg-cells the more recent determinants as to head- and breast-feathers—though in the

ascending line through selection—yielded to the old-established combinations? After a period of nutrition, however, they were strong enough to assert themselves. Give them time, Prof. Ewart says, and they will become so prepotent that they may hand on all the peculiarities even when the pigeon is crossed with another breed.

Similarly, the first fertilised almost immature ova of a rabbit, liberated by an ovulation subsequent to the first serving, result in offspring which take after the male. In the fertilisational struggle the paternal determinants have the mastery. If, on the other hand, a doe is served, not at the right time, but a week or ten days after, when the next young come they are all exactly like the mother. The expression of inheritance is after the parent whose germ-cells were the riper.

These results, Prof. Ewart said, "were altogether different from Weismann"; from another point of view they are altogether illustrative of Weismann's theory of germinal selection.

Conclusion.—If we accept the concept of ancestral plasms—that is to say, the idea that an inheritance is a mosaic of ancestral contributions, and that a complete hereditary equipment is present not merely in dual but in multiple form within the fertilised egg—then we pass naturally enough to the idea of a struggle among the hereditary tendencies, which Darwin indeed suggested—which Weismann, however, has elaborated into a fascinating hypothesis.

If there are multiple analogous but not identical determinants corresponding to any independently variable and heritable part of the organism, what is to decide the expression of these? It is plain that the organism is not usually a *mêlange* or blend of the ancestral contributions which made up its inheritance. Must we, then, simply fall back on the general assumption of a regulative entelechy which determines the determinants? In other words, perhaps, is the mysterious unity of the organism, which applies to the fertilised egg-cell as well as to the full-grown creature, such that it determines, by the very fact that there is a unified organisation, which determinants

shall be in the foreground and find expression, and which shall remain in the background, and latent? Or is it enough to suppose that the cytoplasmic soil—the cell—in which the analogous determinants find themselves, and environmental influences in the widest sense, decide which determinants are to be liberated and to find expression? Weismann suggests that we may reach a clearer possible image of occurrences if we introduce the concept of struggle.

The analogous determinants need not all be of equal strength, and when they liberate their biophors in the appropriate area there may be a struggle amongst these; or long before it comes to the actual liberation and dissolution of determinants there may be a struggle between them. They are by hypothesis living units, feeding, growing, and multiplying, and if there are inequalities amongst them, as there may well be, since some are older and others younger and since they have had diverse histories, then there may be struggle amongst them, and here too—as in the wider world of nature—the weaker may go to the wall. Moreover, the analogous determinants need not be all different from one another; similars may, so to speak, support one another in development, while incompatibly different forms may be in a minority and have little chance of asserting themselves. All this is apt to become anthropomorphic speculation, but then the determinants are *alive*.

CHAPTER XIII

HEREDITY AND SEX

§ 1. *Relations between Sex and Inheritance.*
§ 2. *The Determination of Sex.*
§ 3. *Different Ways of Attacking the Problem.*
§ 4. *Classification of the Theories.*
§ 5. *First Theory: Environment Affects Offspring.*
§ 6. *Second Theory: Fertilisation is Decisive.*
§ 7. *Third Theory: Two Kinds of Germ-cells.*
§ 8. *Fourth Theory: Maleness and Femaleness are Mendelian Characters.*
§ 9. *Fifth Theory: Nurtural Influences Operate on the Germ-cells through the Parents.*
§ 10. *Another Way of Looking at the Facts.*
§ 11. *Conclusion.*

§ 1. *Relations between Sex and Inheritance*

THE main question here is: What determines sex? but there are some accessory questions.

(*a*) Whatever "maleness" and "femaleness" may imply in final analysis, there seems no doubt that a single germ-cell may contain the potentiality of them both, and of all the masculine and feminine characters as well. The drone-bee has a mother, but no father, and many other instances are known of unfertilised eggs developing into males, whose quality of maleness and masculine characters are handed on through their daughters to their grandsons.

(*b*) The differences between man and woman, peacock and peahen, ruff and reeve, stag and hind, lion and lioness, are so conspicuous and manifold that we are apt to lose sight of the primary distinction that the male is a sperm-producer and the female an egg-producer. In the lower reaches of the animal kingdom the two sexes are often superficially alike; it is as we ascend the series that the primary differences have all manner of secondary differences added to them. We hold to the central thesis of *The Evolution of Sex* (1889) that there is a deep constitutional difference between the male and the female organism—a fundamental difference in metabolic gearing—the female being relatively more constructive or anabolic, the male relatively more disruptive or katabolic. This difference in the organism is an expression of a similar deep initial difference in the fertilised ova, which determines whether they get on to male or female lines of development. The getting on to male or female lines of development determines, late or early, whether the detailed characters will find a masculine or a feminine expression.

(*c*) In some cases, notably in insects, the differentiation of the secondary sex-characters occurs at the same time as the differentiation of the reproductive organs, and it cannot be said at present that the latter influence the former. Both may be simultaneous and independent expressions of the same initial differences in the fertilised ova.

In other cases, certainly, it is the saturating influence of the early established maleness or femaleness that determines the development of detailed parts, and of habits as well as structure. A castrated pullet may acquire not only the outward structural features of the opposite sex—cock's comb, wattles, long hackle and tail feathers, rapidly developing spurs, carriage, etc.—but the behaviour as well and the pugnacious character. There is rapidly accumulating evidence of the importance of internal secretions or hormones which pass from the reproductive organs and exert a pervasive influence in development. One can argue

from an abnormality of an antler to an abnormality of a testis. If a merino male lamb be castrated the adult is hornless like the female. We are led to the idea that what is actually inherited may be in many cases common to the two sexes, but is capable of masculine or feminine expression according to the liberating stimuli which activate it.

(*d*) Of much interest in this connection is the occurrence of what are called "sex-limited characters." Colour-blindness in mankind is a familiar example. It is much commoner in men than in women. But the colour-blind man with a quite normal wife does not have colour-blind children. His sons are normal and his daughters *apparently* normal; but the condition is transmitted through the daughters to half their sons.

In Plymouth Rock poultry with alternate light and dark bars on the feathers, the barred character illustrates sex-limited inheritance. When a male is crossed with a non-barred breed, the offspring are all barred, whether male or female. This means that the male Rock is homozygous, that all his germ-cells bear the determinant of the barred character. When a female Rock is crossed with a non-barred breed, the offspring are half-barred (the males) and half non-barred (the females). This means that the female Rock is heterozygous as regards barred-ness, that half of her germ-cells have and half have not the determinant of the barred character. But there is the further point that in her germ-cells there is some linkage between male-producing and the barred character, between female-producing and the absence of the barred character.

Another instance may be given. When Dorset sheep, horned in both sexes, are crossed with Shropshire sheep, hornless in both sexes, horns occur on the male offspring, but not on the female. The horn-producing character is dominant in the male sex, recessive in the female. When the hybrids are interbred, their progeny—the F_2 generation—include hornless males and horned females—both breeding true—as well as horned males and

hornless females, which may be *either* pure or impure, homozygous or heterozygous.

§ 2. *The Determination of Sex*

The Determination of Sex is one of the great unsolved problems of Biology. It seems to be peculiarly elusive, but perhaps that simply means that it is near the central secret of life itself. Over and over again the solution has slipped through the fingers of Science just when they seemed to be closing upon it. Perhaps this means that we have not yet learned how to ask the question rightly. Perhaps the problem is very complex, with different answers in different cases ; perhaps the solution is, after all, very simple.

A Multitude of Theories.—From ancient times a keen interest has been taken in the question of the determination of the sex of the offspring, and of the answers that have been proposed it may well be said that "their name is legion." For many of the answers are bound up with "theories of sex," which are also legion. It is quaint to notice that the number of speculations connected with the nature of sex has been well-nigh doubled since Drelincourt, in the eighteenth century, brought together two hundred and sixty-two "groundless hypotheses," and since Blumenbach caustically remarked that nothing was more certain than that Drelincourt's own theory formed the two hundred and sixty-third. Subsequent investigators have at least tried to add Blumenbach's theory of a fundamental "Bildungstrieb" or formative impulse to the scrap-heap.

The numerous answers offered to the question : What settles the sex of the offspring ? might be arranged on an inclined plane so as to illustrate the progress of natural knowledge. "As in so many other cases, the problem of the determination of sex has been looked at in three different ways. For the theologian, it was enough to say that 'God made male and female.' In the period of academic metaphysics, still so far from ended, it

was natural to refer to 'inherent properties of maleness and femaleness'; and it is still a popular 'explanation' to invoke undefined 'natural tendencies,' to account for the production of males or females. Thirdly, it has been recognised that the problem is one for scientific analysis" (Geddes and Thomson, *Evolution of Sex*, 1889, revised edition 1901, p. 35).

Even after the problem of the determination of sex was recognised as one that must be tackled scientifically, or not at all, the suggestions offered have varied greatly in their consistency of adherence to scientific method. There are still frequent appeals to "natural tendencies," and these must be judged, not by their self-explanatory character (for biological formulæ will never be that), but by their correspondence with the limits of available physiological analysis, and by their applicability in the actual control of life.

There is a library of books and pamphlets dealing with the determination of sex, but a large number—redolent as they are of good intentions—must be set aside at once because of *obviously fatal* defects in their scientific procedure. Some lay stress on what even the most tolerant must admit to be at least *unverifiable* factors, such as the desire of the parents or parent to have a male child. Others allege the operation of factors which are physiologically absurd. Others base a generalisation on an outrageously small number of cases. The reason for the unusual copiousness of speculation in regard to this difficult biological question is to be found rather in its practical than in its theoretical interest.

The Problem Stated.—The general problem is: What determines whether a fertilised egg-cell will develop into a male or a female organism? But let us look at particular forms of the problem. What are called identical or monozygotic twins arise from the division of a developing ovum into two independently developing areas, and they are always of the same sex, identical in this as in their other features. But ordinary twins, which

arise from two distinct ova developing simultaneously, are often of different sexes. Why is there this difference? The same question arises when we contrast the "poly-embryony" (*i.e.* numerous embryos from one ovum) which occurs in some insects with the ordinary simultaneous production of many offspring from as many ova. In poly-embryony the offspring are all of the same sex; in ordinary multiparity both sexes occur in varying proportions. As we shall see, this particular case of the general problem is very suggestive.

In one household the family consists of boys and girls, in a second of boys only, in a third of girls only—what determines this? A setting of hen's eggs gives rise to cocks and hens in varying proportions—is the proportion practically modifiable? A guillemot usually lays a single egg in a season—what determines the sex of the offspring? It is well known that the unfertilised eggs of a queen-bee develop into drones, while the unfertilised eggs of aphides produced all through the summer months develop into parthenogenetic females, until at the end of the season, in autumn, males are produced. What does this mean?

A great step would be gained if we could narrow the issue in various cases by answering the question, *When* is the sex of the offspring finally determined? How long may a germ-cell remain with the potentiality of either sex? Is there sex-determination before fertilisation or during fertilisation, or not until after fertilisation? Are there cases where we must admit that the embryo has the potentiality of *either* sex? Is the determination early in some types, such as Mammals, and later in other types, such as Amphibians?

Prof. V. Haecker has proposed a useful terminology. Sex-differentiation implies that one of the two sex-primordia in the germ-cell is activated, while the other remains latent. (*a*) This may occur before fertilisation—*progamic* sex-differentiation—as in the large and small ova of Dinophilus, Rotifers, and Phylloxera. (*b*) Or it may occur at the moment of fertilisation—*syngamic*

sex-differentiation—as in the case of the hive-bee, where the fertilised ova become queens and workers and the unfertilised ova drones. (*c*) Or it may (theoretically) occur after fertilisation at some stage in development—*epigamic* sex-differentiation. But the examples of this that used to be cited have given way before criticism, and no convincing case is at present known.

Here we may refer to Prof. E. B. Wilson's proposal to draw a distinction between sexual predetermination and sexual predestination. "The definitive determination of maleness or femaleness only occurs when all the factors necessary to their production have been brought together. This *may* be effected before fertilisation ('progamic determination' of Haecker), but may also first ensue upon union of the gametes ('syngamic determination'). Thus one may suppose that all the sexual eggs of a queen-bee and of Maupas' *Hydatina* are predestined towards *maleness*, but this is reversed by fertilisation when determination occurs."

§ 3. *Different Ways of Attacking the Problem*

The problem of the determination of sex has been attacked scientifically along three distinct lines, which are complementary, not opposed. In some cases there has been a combination of two methods.

Statistical.—Some conclusions as to the determination of the sex of the offspring have been based on statistics, *e.g.* of the relative numbers of male and female offspring in different localities, at different times, with different ages of parents, and so on. These statistics are valuable in proportion to the breadth of their base, but it must be remarked that great care is necessary in giving a *physiological interpretation* of statistical results.

Cytological..—Some conclusions as to the determination of the sex of the offspring have been based on observations of the germ-cells in particular cases. Thus it has been shown that some animals have two kinds of ova, the larger developing into females.

In the rabbit it is possible, according to Russo, to distinguish two kinds of ova in the ovary. According to Riddle there are

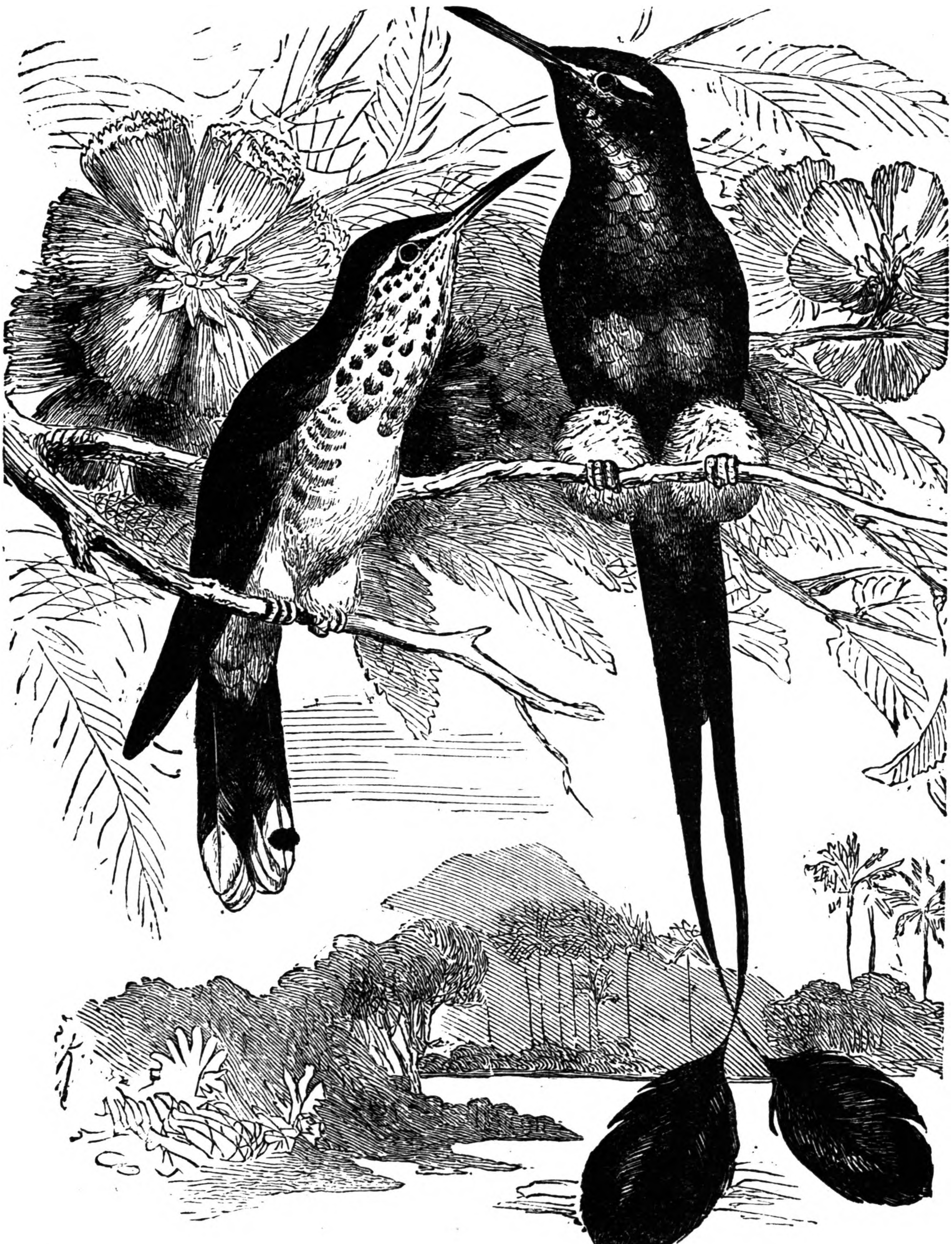

FIG. 45.—Decorative male and less adorned female of Spathura—a genus of Humming-brids. (From Darwin, after Brehm.)

male-producing and female-producing ova in pigeons, differing in their regime of metabolism. Dimorphism of spermatozoa is not uncommon. In some cases the size-dimorphism of sperms is asso-

ciated with the fact that one half of the spermatozoa have "an accessory chromosome," absent in the other half. Apart from size-dimorphism, the occurrence of an accessory chromosome in half of the spermatozoa has been observed in numerous and varied types of animals. There is interesting indirect evidence that the ova fertilised by spermatozoa with the accessory chromosome develop into females, while those fertilised by spermatozoa without the accessory chromosome develop into males.

Experimental.—Some conclusions as to the determination of the sex of the offspring have been based on experiment, *e.g.* subjecting the eggs, or the embryos, or the parents to particular conditions of nutrition, temperature, and the like, and observing whether the relative numbers of the sexes in the offspring are in any way different from those obtaining in ordinary conditions; or by contrasting the results of fertilising immature and over-ripe ova; or by trying particular breeding experiments in reference to what are called sex-limited characters.

§ 4. *Classification of the Theories*

There are two main alternatives: (i) Are there two kinds of germ-cells (male-producing and female-producing), which are, in their occurrence and in their development, quite unaffected by environmental influence? *or*, (ii) Do environmental influences give the germ-cell, either in its early stages or during its development, a bias towards male-production or female-production?

But a more detailed classification may be clearer and more convenient for discussion. Five theories may be distinguished.

(*a*) That environmental influences, operating on the sexually undetermined offspring (after fertilisation), may at least have a share in determining the sex.

(*b*) That the sex is undetermined until the germ-cells unite in fertilisation, when it is decided by their relative condition, or by a balancing of the tendencies they bear, neither sperm nor ovum being necessarily decisive.

(*c*) That the sex is fixed at a very early stage by the constitu-

tion of the germ-cells as such, there being female-producing and male-producing germ-cells, predetermined from the beginning and arising independently of environmental influence.

(*d*) That maleness and femaleness are Mendelian characters.

(*e*) That environmental and functional influences, operating through the parent's body, may alter the proportion of effective female-producing and male-producing germ-cells.

It will be seen that these five theories are not in a strict way mutually exclusive. Even if we conclude that there are,

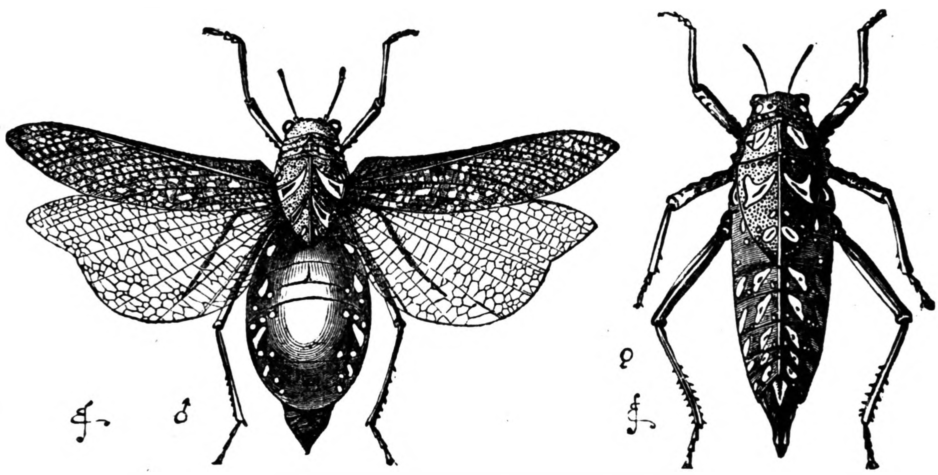

FIG. 46.—Winged male and wingless female of Pneumora, a kind of grasshopper. (From Darwin.)

for instance, two kinds of ova in the ovary, one set predestined to develop into males and the other set predestined to develop into females, it does not follow that the relative numbers of these may not be changed as life goes on, *e.g.* by the diet of the parent. And even if we conclude that there are two kinds of ova predestined from the start, it does not follow that the predestination need be quite unalterable by the conditions of fertilisation and of development.

Another preliminary caution must be noted. One must be careful in arguing from one set of organisms to another. What determines sex in frogs may not hold true for cattle; what determines sex in Rotifers may not apply to birds. Nature

is very manifold, and it may be that sex is determined by a variety of factors operative in different cases and at different stages.

§ 5. *First Theory:—That environmental influences, operating on the sexually undetermined offspring (after fertilisation), may at least have a share in determining the sex*

In many young organisms it is for a time impossible to distinguish the sexes, and the assumption is often made that there is a prolonged indeterminateness as regards sex. The first theory that we need discuss is, as stated above, that environmental influences give the bias towards maleness or femaleness.

In support of this theory it has been customary to refer to the interesting experiments on tadpoles made by Professor Emile Yung, of Geneva, and although these are not so convincing as some have thought, it is due to this zoologist to recognise that he began experimental investigation of the subject at a time when this mode of approach was little thought of.

Let us recall some of Yung's evidence. Tadpoles are said to linger for some time in a state of sex-indifference or potential hermaphroditism. In normal conditions there are about 57 females to 43 males in the hundred. But tadpoles fed with beef, fish and frog-flesh, yielded respectively 78, 81 and 92 females in a hundred. This was, of course, a very interesting result, but it has been pointed out that Yung did not pay sufficient attention to differential mortality, that he had not sufficiently large numbers, and that although some tadpoles are potentially hermaphrodite (with testes around the ovaries), there are others which are quite distinctly male or female even in young stages. But the most important criticism is the first, which leads Beard, for instance, to say that Yung's experiments are only of importance in regard to the relative viability of the two sexes. It is necessary to have renewed experiments on a large scale, and to

have more precise data as to the time when the sex of the tadpole is unmistakably distinguishable.

When a crowd of caterpillars are under-fed, there is an unusually large proportion of males (Landois, Treat, Gentry, and others). But as it was shown long ago that the sex is determined in the larva before it leaves the egg, the starving experiments were irrelevant. They only show that there may be great differences in the rate of juvenile mortality in the two sexes. Thus Prof. Poulton points out in regard to the poplar hawk-moth (*Smerinthus populi*), for instance, that the female caterpillars, being larger, require more food, and will therefore die first when supplies are scarce.

Nor is there agreement among the results of experiment. Kellogg and Bell found that the sex of the silkworm is not appreciably affected by the nutrition of the parents or even grandparents. Cuénot found that the proportion of the sexes in blow-flies, where its visible determination is later than in butterflies, was not affected by what the larvæ ate, or by what their parents ate.

What then is our conclusion in regard to the first theory? It must be admitted that there is no cogent evidence to show that environmental influences operating on a developing organism may decide what its sex is to be. Yet we should be slow to assert that this is impossible. Consider, for instance, Nussbaum's elaborate experiments on *Hydra grisea*, which he subjected to varying nutritive conditions. In this species there are both hermaphrodite and diœcious forms. Nussbaum found that the optimum nutritive conditions resulted in predominance of female polyps, and that groups wholly male could be produced by relative starving. From these experiments it seems that in Hydra the nutrition of the body determines the production of ovary or testis.

There are analogous experiments in regard to some plants. Prantl found that spores of the Royal Fern (*Osmunda*) and of

Ceratopteris thalictroides sown in soil without nitrogenous supplies developed into male prothallia, that female organs were formed when ammonium nitrate was supplied, and that wholly male prothallia might become wholly female prothallia. Similar results have been obtained for horsetails by Buchtien.

It is plain, of course, that in cases like fern-prothallia and Hydra, which are normally hermaphrodite, what actually occurred in the experiments was the inhibition or suppression of one set of sexual organs in favour of another. None the less do the experiments suggest that the first theory is not to be dismissed too hurriedly.

Moreover, when we recall how a little nutritive attention makes a worker-grub a queen-bee, or how Aphides produce females parthenogenetically through months (or even years) of high feeding and pleasant temperature, and how the advent of autumn, with its cold and its scarcity of food, is followed by a birth of males, and so on, we may not be able to share the dogmatism of some who assert that the theory of the environmental determination of sex is preposterous. We shall consider later on the question of the influence of the environment on the parents.

§ 6. *Second Theory :—That the sex is undetermined until the germ-cells unite in fertilisation, when it is decided by their relative condition, or by a balancing of the tendencies they bear, neither sperm nor ovum being necessarily decisive*

It has been a favourite theory, especially in regard to man and mammals, that the sex of the offspring depends upon the relative condition of the germ-cells at fertiiisation, the differences in condition depending on the relative age of the parents and other such circumstances. Let us consider various forms of this second theory.

Hofacker (1828) and Sadler (1830) independently published

statistics in support of the theory that when the male parent is the older the offspring are preponderatingly male, and that when the female parent is the older the offspring are preponderatingly female. In short, the sex of the offspring depends on the relative ages of the parents. Statistical evidence has been found supporting and contradicting this theory. Schultze's experiments on mice tell strongly against it.

Yet it seems fair to notice, that if the germ-cells remain for some time undetermined in regard to the sex which they will express—if, in other words, they retain for some time the potentiality of either—there is no *a priori* reason against the theory that the absolute and relative ages of the parents may have influence.

Or, again, even if there are two kinds of egg-cells and two kinds of sperm-cells, which are from the first determined towards female-production or towards male-production, the age of the parent may favour the production of one kind rather than of the other, or may favour the survival of one kind rather than of the other.

It is hazardous for the inexpert to draw conclusions from statistics, but there seems evidence in mankind of a correlation between the age of the mother and the sex of the child. The younger mothers tend to have more female children; the older mothers tend to have more male children. On this the self-regulating balance of sex in a nation depends. When females are scarce—for instance, in a colony—they mate early, and supply the demand for girls. When men are scarce—for instance, after war—there are more late marriages, and therefore more boys.

In connection with the general importance of age as a reproductive factor, reference should be made to the remarkable work of Dr. Matthews Duncan, *Fecundity, Fertility, Sterility, and Allied Topics* (Edinburgh, 1866).

By many authors, *e.g.* Girou, and at various dates, the theory has been propounded that the sex of the offspring tends

to be that of the more vigorous parent. This is a favourite opinion among breeders and among the fathers of many boys, but it lacks substantiation, and the concept of comparative vigour is too vague to be useful.

So far as parental vigour may depend on what may be called strained reproduction, or on deterioration supposed to result from close in-breeding, Schultze's experiments on mice do not in the least confirm the view that it has any effect on the proportions of the sexes.

Starkweather was responsible for the theory that the sex of the offspring tends to be the opposite of that of the "superior" parent; but "superiority" and "comparative vigour" are far too vague to be scientifically discussable. Dr. Marshall notes that Allison, an authority on the thoroughbred horse, accepts Starkweather's theory. So far as we have been able to discover there are not any secure facts warranting the idea that a prepotent sire gives his offspring a bias either towards his own sex or towards the opposite.

Van Lint maintains that the offspring has the sex of the sexually weaker parent, *i.e.* the parent whose sex-cells are relatively the weaker at the time of fertilisation. If a relatively feeble ovum is fertilised by a relatively vigorous spermatozoon, the embryo will be a female, but its body will follow the father. The author explains under six heads what is meant by being sexually weaker or stronger, but he naïvely points out that the sure and certain sign of a man's being more sexually vigorous than his wife is his having a daughter. "Le sexe de l'enfant tranchera la question." The theory lacks scientific backing.

It has been repeatedly suggested that a determining factor may be found in the relative maturity or freshness of the sex-cells which unite in fertilisation. Thury and other breeders have maintained that an ovum fertilised soon after ovulation is likely to produce a female. That is to say, the fresher ovum, not exhausted in any way, *e.g.* by continuing to live without feeding,

will tend to produce a female. An older egg tends to produce a male. The bias of the ovum may be corroborated or contradicted by the condition of the fertilising spermatozoon.

As the outcome of a very large series of experiments, Prof. Richard Hertwig found that either over-ripeness or under-ripeness of the eggs (due to artificially delaying or hastening fertilisation) led to a large excess of males. Elaborate experiments by Sergius Kuschakewitsch have corroborated Hertwig's results up to the hilt. The proportion of males is largely dependent on the degree of over-ripeness in the ova, and cultures of males only—with only 4–6 per cent. of deaths—were obtained.

In connection with fertilisation we may notice a theory that has been suggested by Prof. H. E. Ziegler. He assumes that the chromosomes derived from a grandmother tend to produce a female, and those derived from a grandfather tend to produce a male. He points out that the parental chromosomes include contributions from grandfather and grandmother, and since the relative numbers of these depend on the chances of the reduction division in maturation, it will be a "toss-up" whether grandfatherly or grandmotherly chromosomes predominate. If the former, the child will be a boy; if the latter, a girl.

Probably, however, this speculation is inadmissible. We must rid our minds of the view (held by many in the past) that there is in ordinary cases any necessary *intrinsic* bias in the egg to produce a female, any necessary *intrinsic* bias in the spermatozoon to incite the development of a male, and that there is *thus* a combination of maleness and femaleness in the fertilised egg. It is enough to recall the fact that the drone-bee has a mother but no father, and the same is true of many Hymenoptera. This is but a striking instance of the numerous facts which lead one to conclude that every germ-cell—whether ovum or spermatozoon—has in it the potentiality of the distinctive characters of both sexes. At some stage or other, we seem

bound to conclude, something occurs, perhaps a fixing of the metabolism-rhythm, perhaps some alteration of the ratio between nucleoplasm and cytoplasm, perhaps the introduction of a specific qualitative sex-determinant in fertilisation, which decides whether the organism will become a male or a female and whether masculine or feminine hereditary characters will find expression.

Our conclusion in regard to the second theory must be—That there is little warrant for attaching much importance to the relative condition of the germ-cells at the time of amphimixis. The experiments of such a careful worker as Richard Hertwig incline one to keep the question open, though O. Schultze's results seem to close it in one case at least. He experimented with enormous numbers of mice, which are very good subjects, being ready to breed when seven weeks old, and littering, it may be, every three weeks, if not allowed to suckle. He found that the proportions of the sexes were unaffected by the age of the parents, by apparent vigour, by consanguineous unions, by frequency of births, or by any kind of nutritive change.

§ 7. *Third Theory:—That the sex is fixed at a very early stage by the constitution of the germ-cells as such, there being female-producing and male-producing germ-cells, constitutionally pre-determined from the beginning.*

On this view there are two kinds of germ-cells, constitutionally pre-determined to be female-producers or male-producers. This implies that the sex is determined before fertilisation, thus excluding the *second* theory. It also implies that the influence of the environment is negligible after the germ-cells have been established, and *a fortiori* after development has begun, thus excluding the *first* theory.

Two Kinds of Ova.—It may be that there are two kinds

of ova—one kind constitutionally predestined to developing into males, the other kind constitutionally predestined to developing into females. This view is not inconsistent with the assumption, which seems almost inevitable, that all ova carry a complete hereditary equipment of both masculine and feminine characters, though only one set usually finds expression. But what evidence is there of two kinds of ova?

Some animals normally produce two *sizes* of ova. Thus, in *Phylloxera* among insects, and *Hydatina senta* among Rotifers, there are large eggs which develop into females, and small ones which develop into males. As both develop without fertilisation, the problem is not complicated by the influence of the sperm.

In *Dinophilus apatris*, according to Von Malsen, and in a mite, *Pediculopsis*, according to Reuter, where fertilisation occurs as usual, there are large ova which develop into females and small ova which develop into males. In *Dinophilus* the ovum which becomes a male is only about one-tenth of the size of that which becomes a female; and the male himself is a degenerate pigmy!

Perhaps the occurrence of two sizes of ovum is much commoner than we know. Thus Baltzer has recently described it in sea-urchins. But we must not hastily assume that it is the size that determines the sex, since it may be that the constitutional predisposition to one sex or the other determines the size. On our own theory, the ovum of relatively greater anabolic bias—predestined to develop into a female—will tend to gather into itself more reserve material than one predestined to develop into a male. It seems probable that the size marks, but does not make, the difference.

Of great importance is the work of Riddle (see p. 618), showing that in pigeons there are eggs with high storage metabolism which develop into females, and eggs with a low storage capacity which develop into males.

In some of the higher Pteridophytes there are two kinds of spores, micro- and macro-spores, which produce respectively male and female prothallia. Prof. E. B. Wilson notes that a similar predestination, not marked by visible differences, has been proved by Blakeslee in both zygotes and spores of various species of fungi, and that it has also been demonstrated in liverworts and mosses. He refers in particular to the recent studies of the Marchals on diœcious mosses. "Isolation cultures prove that the asexual spores, though similar in appearance, are individually predestined as male-producing and female-producing; and all efforts to alter this predestination by changes in the conditions of nutrition, such as are known to be effective in the case of fern prothallia, failed to produce the least effect."

The view that there are two kinds of ova, determined *ab initio* as male-producers and female-producers, has a vigorous supporter in Beard, who finds evidence in the skate. He maintains that the sex is determined when the primitive germ-cells divide into oocytes. In his 1902 paper on "The Determination of Sex in Animal Development," Beard scouted the idea of environmental interference with the determination of sex. "Any interference with, or alteration of, the determination of sex is absolutely beyond human power. To hope ever to influence or modify its manifestations would be not less futile and vain than to imagine it possible for man to breathe the breath of life into inanimate matter." To this, an experimenter like Russo would answer that he *has succeeded* in effectively interfering with the determination of sex. Although it may not be possible to alter the bias of an egg which has become fixed as a male-producer or a female-producer, it may be possible by altered nutrition to change the proportions of these two kinds of eggs in the maternal ovary, and it may be possible in other ways to change the normal proportions of survival.

Of great interest in connection with the third theory are the facts of poly-embryony—the production of multiple embryos

from one ovum. Like "identical twins," the "poly-embryonic" offspring are always of the same sex. In the Nine-Banded Armadillo it is certain that quadruplets normally arise from segregations in the germinal area of one ovum, and these are always of one sex. In some of the parasitic Hymenopterous insects, *e.g. Encyrtus*, investigated by Marchal and Bugnion, *Litomastix* and *Ageniaspis*, investigated by Silvestri, one segmented ovum forms a group of embryos, all of the same sex—female if the egg be fertilised, male if it be not fertilised. Now, it cannot be denied that these facts strongly confirm the view that the sex of the offspring is already determined in the egg.

The theory has been more than once suggested that the ova from one ovary develop into females and those from the other ovary into males. Thus Dr. Rumley Dawson (*The Causation of Sex*, London, 1909) has maintained, for man, that the ova produced by the right ovary develop into males, and that those produced by the left ovary develop into females. This view has been tested experimentally in the rat by Doncaster and Marshall, who found that each rat, with one ovary completely removed, produced young of both sexes. "This does not, of course, prove that 'the right and left ovary hypothesis' is not true for man, but its definite disproof for another mammal detracts from its probability." The theory has also been disproved in Amphibians by H. D. King, and that it cannot apply to birds is obvious, since they have only one ovary.

Two Kinds of Spermatozoa.—In about thirty different kinds of animals, such as the freshwater snail, *Paludina*, and the freshwater beetle, *Dytiscus*, there are two kinds of spermatozoa which differ from one another in certain details of form. It has been suggested that each kind is predestined towards the development of one sex, but there is no definite evidence that the dimorphism has this significance.

The theory that in Vertebrates one testis yields male-producing spermatozoa, the other female-producing spermatozoa,

has been disproved in rats by Copeman. Moreover, as Doncaster and Marshall point out, it is known to stock-breeders that bulls from which one testicle has been removed continue to give calves of both sexes.

The Accessory Chromosome.—Of great interest are the facts that have recently come to light regarding what is called *the accessory chromosome.* In a number of insects, Myriopods and Arachnids, the females have more chromosomes in their cells than the males have. In the simplest cases (*Anasa, Protenor*) the female has one more chromosome than the male, and the egg has one more likewise. Now, half of the spermatozoa differ from their neighbours in having the same number of chromosomes as the egg, while the others have one fewer. This extra chromosome which half have and half have not is called the X-element or accessory chromosome. There are facts which go to show that fertilisation of the eggs by one class of spermatozoa results in males, by the other in females. When two equal numbers come together, the result is a female.

In the squash-bug, *Anasa tristis,* studied by Wilson, the eggs have 11 chromosomes and the sperms 10 or 11. Egg 11 + sperm 11 produces a fertilised egg with 22 (2N) which develops into a female. Egg 11 + sperm 10 produces a fertilised egg with 21 (2N − 1) which develops into a male.

The chromosomic dimorphism has been proved in about a hundred species, but all are not equally convincing, and there are many variations in detail. As the subject is difficult, especially without diagrams, and as the facts have been repeatedly summed up in the last few years (*e.g.* by Wilson, who has contributed more than any other to the investigation), we do not propose to do more than refer to two or three important points.

(*a*) In many cases, instead of there being an accessory chromosome in one half of the spermatozoa and no corresponding body in the other half, there is a " large idiochromosome " or X-element

in one half, and a " small idiochromosome " or Y-element in the other half.

(*b*) The evidence that the one set of spermatozoa induce male-development and the other set female-development is indirect; it is obtained by an examination of the state of the chromosomes in the body-cells of the offspring. The Y-element, for instance, is found only in the males, while the X-element is found in both sexes, but doubled in the female, single in the male.

(*c*) Wilson gives the following formulæ:—

(*a*) In the absence of a Y-element.
Egg X + spermatozoon X = zygote XX (female).
Egg X + spermatozoon no X = zygote X (male).

(*b*) In the presence of a Y-element
Egg X + spermatozoon X = zygote XX (female).
Egg X + spermatozoon Y = zygote XY (male).

In the German cockroach (*Blatta germanica*) and in the " Red Bug " (*Pyrrhocoris apterus*), half of the spermatozoa have the same number of chromosomes as the ripe ova (N), including the accessory chromosome; the other half have one less (N — 1), being without the accessory chromosome. An ovum with N, fertilised by a spermatozoon with N, results in a fertilised ovum with 2N, and this develops into a female. An ovum with N, fertilised by a spermatozoon with N — 1, results in a fertilised ovum with 2N — 1, and this develops into a male.

In the meal-worm (*Tenebrio molitor*) and in the house-fly (*Musca domestica*) the number of chromosomes is the same throughout, but in half of the spermatozoa one of the number is small, and ova fertilised by these develop into males.

A fine corroboration of the importance of the chromosomes

has been recently afforded by the work of T. H. Morgan on *Phylloxera* and of von Baehr on *Aphis saliceti*. In these forms half of the spermatocytes degenerate (as Meves pointed out in the bee), namely those without the accessory chromosome; therefore all the spermatozoa are female-producers, and every one knows that all the fertilised ova produce females. An interesting accessory discovery is that in *Phylloxera* and Aphides the males have in their bodies one chromosome fewer than the females have. "The male-producing egg," Wilson notes, "must therefore eliminate one chromosome, and this, we cannot doubt, is the X-element."

These cytological studies are so very striking that one inquires eagerly as to the distribution of the phenomena in the animal kingdom. There have been some noteworthy recent extensions.

An accessory chromosome is reported by Boveri and Gulick in *Heterakis*, a Nematode of the pheasant. The ovum has five chromosomes; the sperms are of two types, one with four, the other with five—a condition similar to that described by Wilson for *Protenor*, one of the Hemiptera. In the common *Ascaris megalocephala* there is also evidence of an accessory chromosome, but it seems at present somewhat discrepant and difficult. There are many other cases now known. As one would expect from the difficulty of the inquiry, there is still considerable discrepancy of description in regard to many cases in which an accessory chromosome has been affirmed. In a variety of types, *e.g.* house-fly and pig, it has been shown that the presence or absence of an accessory chromosome in the spermatozoa is associated with size-dimorphism.

Accessory chromosomes have been demonstrated in numerous vertebrate types, *e.g.* the Amphibian Necturus, guinea fowl, common fowl, armadillo, opossum, bat, rat, white mouse, guinea-pig, sheep, horse, pig, bull, cat, dog, and man himself.

The theory that the presence of one X-element in a fertilised ovum means male offspring, and that the presence of two means female offspring, is morphological, and our physiological sense is left unsatisfied. Is the difference significant in itself, or as an index of metabolic differences? If the eggs with more chromatin than their neighbours develop into females, and if chromatin be an index of a relatively preponderant anabolism or anabolic capacity, can the theory be brought into line with the thesis of *The Evolution of Sex*, that the female is the outcome and expression of relatively preponderant anabolism, and the male of relatively preponderant katabolism?

Baltzer has observed that about half of the eggs of the sea-urchin are distinguished from the others by having one of the eighteen chromosomes represented by a short "hook-chromosome" instead of a normal "rod-chromosome," and there is indirect evidence that those ova with the short "hook-chromosome" become males. In discussing this case and comparing it with the state of affairs in the various insects already referred to, Boveri points out that in both cases the fertilised ovum from which a female develops has *more chromatin* than that from which a male develops, and that the amount of chromatin has a regulative influence on the amount of cytoplasm. He recalls cases, such as Issakowitsch's Daphnids, von Malsen's Dinophilus, and Russo's rabbits, where it appears to him proved that nurtural conditions influence sex-determination. The better-equipped ova become females. He suggests, therefore, that in some cases nurtural influence operates variably or unequally on sexually indifferent germ-cells, giving them a bias to the one sex or the other, and that in other cases the decision is due to an internal factor such as the presence of stronger "assimilation-chromosomes" in some of the ova.

On the other hand, it may be that the additional chromatin material is of qualitative importance. Thus, to give point to his theory, Prof. E. B. Wilson suggests quite provisionally

that the X-element contains factors (enzymes or hormones ?) that are necessary for the production of both the male and the female characters; that these are so adjusted that in the presence of a single X-element the male character dominates, or is set free; while the association of two such elements leads to a reaction which sets free the female character.

§ 8. *Fourth Theory:—That Maleness and Femaleness are Mendelian Characters*

A Mendelian interpretation of sex, first suggested by Strasburger, has been developed by Castle, Correns, Bateson, and others. As Prof. Wilson points out, the interpretation has taken "three forms, which exhaust the *a priori* possibilities. These are, first, that both sexes are sex-hybrids, or heterozygotes (Castle); second, that the male alone is a heterozygote, the female being a homozygote recessive (Correns); third, that the female is the heterozygote, the male being a homozygote recessive (Bateson)."

As Prof. Wilson has shown, each of these forms of the theory has its special difficulties, which seem to be most serious in the case of the first.

Prof. Correns's theory was based on beautiful experiments in crossing diœcious and monœcious forms of Bryony, which showed that the monœcious condition behaves as a unit character, which is recessive to the diœcious.

The experiments made by Correns go to show that the pollen-grains of the diœcious Bryony, though apparently all alike, must be regarded as of two kinds in equal numbers—male-producing and female-producing. What immediately arise, as a matter of fact, are the rudimentary male prothallia, which produce the reproductive gametes or pollen-nuclei, and the egg-cells fertilised by half of these produce male plants, while the egg-cells fertilised by the other half produce female plants.

The third form of the Mendelian interpretation is supported by a number of very striking facts, especially in regard to the common currant-moth (*Abraxas grossulariata*) and the canary. Let us re-state it very briefly. Assuming that there are sex-determinants or 'factors' of maleness and femaleness, the experimenters suggest (1) that these behave as Mendelian units, femaleness being always dominant over maleness; (2) that female individuals are heterozygous as regards sex (having maleness recessive) and that they give rise to equal contingents of male-producing and female-producing ova; (3) that male individuals are homozygous as regards sex, being without the femaleness factor, and give rise only to male-producing spermatozoa; (4) when a male-producing spermatozoon fertilises a male-producing ovum the result is of course a male, when a male-producing spermatozoon fertilises a female-producing ovum the result is a female, femaleness being by hypothesis dominant over maleness.

The study of sex-limited inheritance in the currant-moth, in the barred Plymouth Rock (and according to some in the canary), suggests the conclusion that the female is the heterozygous sex. But Morgan's study of the inheritance of red eyes and short wings in the pomace-fly (*Drosophila ampelophila*) suggests that the male is the heterozygous sex. It may be, then, that in some organisms it is the one way, and in some the other, as regards maleness and femaleness themselves.

Doncaster refers to the confirmation which the Mendelian theory of sex receives from the results of castration. In Vertebrates the castration of the male may prevent the expression of masculine features, but it does not induce the expression of feminine characters. This may mean that the male is homozygous—that is, purely masculine, without any feminine characters latent. We would, however, point out that in many cases there is a lack of positiveness in the feminine characters; it is masculine characters which are positive and distinctive. In other words, there might be a good deal of latent feminity in the

castrated male without there being much to show for it. It would be extremely interesting to experiment with some case like the Red-necked Phalarope, where the female bird is the more masculine of the two.

When a Vertebrate female is castrated, or when the ovary atrophies, there is often a development of masculine characters. We must refer again to the case of the pullet. Guthrie has shown that a castrated female chicken may acquire not only the outward structural features of the opposite sex—cock's comb, wattles, long hackle and tail feathers, spurs, etc.—but the behaviour as well.

In Crustaceans the course of events is curiously the reverse of what is true of Vertebrates. A female whose ovary has been destroyed by a Rhizocephalous parasite has its secondary sex characters reduced, but a castrated male assumes more or less completely the characters of the female. It may be that in this case the female characters are more positive, *e.g.* the broad abdomen. " If the parasite dies and the host recovers, the ovary of the female may again become functional; but in the male under such circumstances eggs may be produced in the testis. Geoffrey Smith concludes from these observations and from others on the Cirripedes, that the female is homozygous in sex and the male heterozygous. There seems no *a priori* reason," Mr. Doncaster continues, " why this should not be true in the case of Crustacea and flowering plants, while the converse is the case in moths and vertebrates."

The fact that the proportions of the sexes are sometimes very variable, as Heape points out in regard to canaries, does not of itself tell against the view that the ova are determined at an early stage to be male-producers or female-producers. There may be a process of discriminate selection during the maturing of the ova, and we know that in higher Vertebrates the possible ova do not all come to maturity.

That the proportions of the sexes in different types are very

diverse seems at first sight to tell against the idea of an internal automatic production of two kinds of gametes—"against the existence of an intrinsic and uniform mechanism of sex-production and against the specific assumption that sex is transmitted as a Mendelian character." But Prof. E. B. Wilson suggests that this difficulty may be overcome by supposing that there is a disproportion in the number of one kind of spermatozoa (like that which reaches a climax in Aphids, Daphnids, etc., where only the female-producing spermatozoa are left), or that there be a certain proportion of impotent spermatozoa, as is well known to be true of the pollen-grains of some flowering plants, like Mirabilis.

§ 9. *Fifth Theory:—That environmental and functional influences, operating through the parent's body, may alter the proportion of effective female-producing and male-producing germ-cells*

This, like the first theory, admits the importance of nurture (in the wide sense), but supposes it to be influential at an early stage in determining the proportion of effective female-producing and male-producing germ-cells. Supposing that the original germ-cells are, as Mendelian theory would lead us to expect, divided into two camps, male-producing and female-producing, we can readily conceive that nurtural conditions may sometimes influence the relative rate of increase or the percentage of survival in the two groups. Or supposing that the immature germ-cells are constitutionally indifferent, as likely to develop into males as into females, we can readily conceive that nurtural conditions, such as a change in the nutrition of the parent, may sometimes decide their destiny.

It seems fairly clear that there are many cases where this theory of nurtural determination will not apply at all, *e.g.* when numerous young are born at once and show an approximately

equal distribution of the sexes. Or how could it apply, for instance, to such a clutch of eggs as Shufeldt reports in the case of a sparrow-hawk? The first became a male, the second a female, the third a male, the fourth a female, and the fifth a male, in regular alternation. Yet these were produced in a short time from *one* ovary, and were probably fertilised by the same set of spermatozoa.

On the other hand, there are cases where a mother produces a long succession of offspring all of one sex, or produces one son and a long succession of daughters, and so on. Such cases suggest that the constitution of the parent may be of some importance, and we know that the constitution is modifiable by nutrition and the other factors in nurture.

When we pass from general considerations, such as the above, and appeal to the facts, we find an interesting conflict of evidence.

From human statistics some have tried to prove that abundant food favours the production of female offspring, and *vice versa*; but others have concluded, also from statistics, that the parental nutrition is of no moment, unless in bringing about a differential death-rate. The fact that 30 per cent. of human twins are of different sexes seems enough to show that the dieting of the parent is not of great importance. Schenk's notorious theory (1898), that the sex of children could be adjusted by dieting the mothers, rested on entirely insufficient evidence—a very small number of cases. Moreover, he supposed that the sex was determined after conception.

In a statistical inquiry in London Mr. Punnett found that the proportion of male to female infants is lowest in the poorest quarter and highest in the wealthiest, yet the differences are not great, and he concluded that they are due to differential infantile mortality, birth-rate, and probably marriage-rate. He was inclined to believe that "in man, at any rate, the determination of sex is independent of parental nutrition. In any case its influence can be but small."

Careful experiments have been made, *e.g.* by Cuénot and Schultze, on the possible influence of the nutrition of the mammalian parent (*e.g.* mouse) on the sex of the offspring; but the results are all against the reality of this supposed influence, in which, however, some breeders strongly believe. Schultze extended his experiments over three generations, but the high feeding of grandparents as well as parents did not seem to have any influence on the proportion of the sexes among the offspring.

Against these results, however, we have to balance the very important work of Heape, who has brought forward evidence for mammals and birds that peculiarities in nutrition and in other environmental influences may exert *a selective influence* on the germ-cells, affecting the proportion of male-producing and female-producing gametes. "Through the medium of nutrition supplied to the ovary, either by the quantity or the quality of that nutrition, either by its direct effect upon the ovarian ova or by its indirect effect, a variation in the proportion of the sexes of the ova produced, and therefore of the young born, is effected in all animals in which the ripening of the ovarian ova is subject to selective action." . . . "When no selective action occurs in the ovary, the proportion of the sexes of ovarian ova produced is governed by the laws of heredity."

Let us take one of Heape's interesting illustrations. Two aviaries of canaries were kept under different conditions and the proportions of the sexes were found to be notably different. In one case, the aviary was kept at a regular temperature during the breeding season; it was comparatively well lighted and sunned; the birds did not receive specially rich food. In the other case, the temperature of the aviary was allowed to vary considerably during the breeding season; it was in a room facing north and east; the birds had abundance of rich food. "In the former of the two cases," to quote Marshall's summary, "nesting, hatching, and moulting took place earlier, only about half the percentage of loss was experienced, and from the nests

in which all the eggs were hatched, the percentage of males produced was more than three times that which was obtained from the other aviary, in which the environmental conditions were less favourable. The results obtained in each case could not be ascribed to the particular strains of canaries, since an interchange of birds between the aviaries was not followed by any material alteration in the proportion of the sexes in the two environments. It is concluded, therefore, that the ova were subject to a selective action on which depended the proportional differences produced" (*The Physiology of Reproduction*, 1910, p. 645).

As the facts stand at present, they point to the conclusion that if nutritive and other environmental influences are operative, it is, in the main, by affecting the production and the survival of sexually-predestined germ-cells.

Of great interest, and, as it seems to us, of importance are Russo's experiments in treating rabbits with lecithin. They lend support to the view that the germ-cells may be predisposed to one sex or the other by the nutritive condition of the parent, and to the view that the difference between the sexes is primarily a question of the rhythm of metabolism. Russo attaches much less importance to the chromosomes and much more importance to the nature of the metabolism than do most biologists of to-day. He says, in so many words, that he believes the sex of the offspring to depend on the specific metabolism of the germ-cells; and he thinks he has succeeded in artificially altering the metabolism of the ovarian ova, and thus altering the normal proportions of the sexes. In the normal ovary there are well-nourished and ill-nourished ova, and the proportion of the former can be increased by lecithin treatment.

Female rabbits treated by injections of Merks' lecithin (solution of 15–20 per cent. in vaseline oil) developed large ovaries, large Graaffian follicles, ova rich in nutritive material, and eventually an unusual number of female offspring. The sperm may, as

it were, corroborate the bias of the ovum, for the percentage of female offspring is higher when both parents are fed with lecithin. It is not possible to follow the ova and prove that a relatively anabolic one always becomes a female, and never a male, and so on, but the argument from altered proportions seems sound. While the lecithin treatment is followed by an increase in the number of ova of "an anabolic type, rich in lecithin globules," it often happens that the *first* litter after the beginning of the treatment shows a marked preponderance of males. This Russo regards as due to the fact that the injections stimulate the general metabolism and inhibit the degeneration of the ova of the katabolic type, capable of producing males. The increase in the number of females occurs subsequently.

It has been objected to Russo's experiments that one of the two kinds of ova which he distinguishes are ova in the course of degenerative change; that he worked with families of selected rabbits (for it is admitted that some females produce more females than others, though this is not known to be a hereditary character); that the high nutrition should result rather in more offspring than in female offspring; and that the number of experiments did not afford a sufficient basis for the conclusion. The experiments have been repeated by Basile and by Punnett, but with entirely negative results. It is desirable that they should be extended to larger numbers and to a variety of types.

Several experimental investigations support the view that changes in nutrition and other environmental conditions may affect the mother so as to alter the ordinary proportions of the sexes. Then Issakowitsch, working with the parthenogenetic females of the Daphnid *Simocephalus*, von Malsen, working with *Dinophilus apatris*, in which the ova are fertilised, found that differences of temperature affected the proportion of the sexes, apparently by affecting the nutrition of the mothers. Both sets of experiments are the more satisfactory that they seem to be free from any fallacy due to differential death-rate in the young

of the two sexes. It has been pointed out by Walker that production of a preponderance of females when food is abundant and a preponderance of males when food is scarce is an advantageous automatic regulation which natural selection would tend to perpetuate.

Many experiments have been made with the Rotifer *Hydatina senta*, but the results are conflicting. There is a striking sex dimorphism, the males being small and gutless. The females are from birth either male-producers or female-producers; and, according to Maupas and Nussbaum, this is determined before birth, while the female embryo is still within its mother's uterus, by conditions of temperature and nutrition. Well-fed mothers produce females which produce females only; starved mothers produce females which produce males only. According to Punnett's researches, however, changes of temperature and nutrition have no effect; but some stocks give rise to many male-producing females, others to few or none.

Against the theory of environmental influence are Strasburger's numerous experiments on diœcious Phanerogams, such as *Mercurialis perennis*, spinach and hemp. He found that changes in illumination, soil, crowding, and so on, had no effect in altering the proportions of male and female offspring. He is of opinion that in such cases the sex is fixed by the time the seed is formed.

As regards the fifth theory, then, we find (*a*) that in certain cases there is some evidence that the nurture of the parents may influence the proportions of the male-producing and female-producing germ-cells, affecting either the number formed or the number that survive, and (*b*) that in other cases there is no hint of any such influence, the facts pointing rather to the view that the sex of the future offspring is not only predestined but predetermined at a very early stage in the germ-cells.

With the facts as they are at present before us, it seems impossible to give any one answer to the question under dis-

cussion. As Prof. T. H. Morgan says: "Admitting that all eggs and all sperms carry the material basis that can produce both the male and female, the two conditions being mutually exclusive when development occurs, the immediate problem of sex-determination resolves itself into a study of the conditions that in each species regulate the development of one or the other sex. It seems not improbable that this regulation is different in different species, and that, therefore, it is futile to search for any principle of sex-determination that is universal for all species with separate sexes; for while the fundamental internal change that stands for the male or the female condition may be the same in all unisexual forms, the factor that determines which of the alternative states is realised may be very different in different species."

Looking back over the array of facts of which we have given samples, we would say, with Dr. F. H. A. Marshall, that they point to the conclusion that "the sex of the future organism is determined in different cases by different factors and at different stages of development—either in the unfertilised gamete, or at the moment of fertilisation, or in the early embryo." We wish, however, to look at the problem from another point of view.

§ 10. *Another Way of Looking at the Facts*

In a recent able article on sex-determination, Prof. H. E. Jordan writes: "The results of the newer investigations on sex-determination seem, at least temporarily, to have brought us back to the position of Geddes and Thomson, namely, that femaleness is causally related to a dominating cell-anabolism, and maleness to a relatively preponderant cell-katabolism. This conclusion would seem to be the base from which future investigations will start in the attempt to further elucidate the fundamental mechanism of sex-differentiation."

To this physiological view of sex, first expounded in *The Evolution of Sex* in 1889, a brief reference must now be made,

for we find ourselves unable to get away from the conviction that there is no sex-determinant or factor at all, in the morphological or in the Mendelian sense, but that what settles the sex is a metabolism-rhythm, or a relation of nucleoplasm and cytoplasm, or a relation between Anabolism and Katabolism.

All through the series of organisms—and of animals in particular—from the active Infusorians and the passive Sporozoa to feverish birds and sluggish reptiles, we read alternatives or antitheses between liberal expenditure of energy and a more conservative habit of storing. This primarily depends on the ratio between disruptive (katabolic) processes and constructive (anabolic) processes, and we regard the sexes as expressions of the same contrast within a given species.

According to this view, the deep constitutional difference between the male and the female organism, which makes of the one a sperm-producer and of the other an egg-producer, is due to an initial difference in the balance of chemical changes. "The female seems to be relatively the more constructive, whence her greater capacity for sacrifices in maternity; the male relatively the more disruptive, whence his usually more vivid life, his explosive energies in action." In short, the sexes express a fundamental difference in the rhythm of metabolism.

As we have seen, many sets of facts lead to the conclusion that each sex-cell has a complete equipment of masculine and feminine characters, and it may be that the liberating stimulus which calls the one set or the other into expression or development, is afforded by the metabolism conditions that have been set up in the field of operations, which lead also to the establishment of ovary or spermary, as the case may be. As Dr. C. E. Walker says in his interesting work *Hereditary Characters* (1910): "The evidence then seems to suggest that the secondary sexual characters are dependent for their development upon the presence of the sexual glands in the individual, and that the potentiality of producing them is present in all individuals of both sexes."

Let us consider the difference between the sexes in its simplest expressions, such as we see, for instance, in Volvox, that beautiful sphere of flagellate cells which well illustrates a body in the making. From the ball of cells reproductive units are sometimes set adrift, which divide to form other colonies without more ado. But in other conditions, when nutrition is checked, a less direct mode of reproduction occurs. Some of the cells in the ball become large, well-fed elements—the ova; others, less anabolic, fade from green to yellow, divide and re-divide into many minute units—the spermatozoa. The large cells of one colony are fertilised by the small cells from another. Here we see the formation of dimorphic reproductive cells in different parts of the same organism. But we may also find Volvox balls in which only ova are produced, and others in which only sperms are produced. The former seem to be more vegetative and nutritive than the latter; we call them female and male organisms respectively; we are at the foundation of the differences between the two sexes.

What we are suggesting is a physiological way of looking at the problem, and the idea that the sex-contrast expresses a physiological alternative. This is suggested in various ways. For instance, there is the sometimes striking evidence that sex is "a quality that pervades all the cells of the organism." Prof. Wilson notes the extraordinary fact—surely of profound importance—that "in the Mosses the Marchals demonstrate that all the products of a single spore are likewise immutably determined, since new plants formed by regeneration from fragments of the protonema, or from any part of the gametophyte, are always of the same sex."

It is very interesting also to consider cases where the sex changes in the course of life! Thus in the hag-fish (*Myxine glutinosa*), according to Cunningham and Nansen, spermatozoa are produced up to a certain size, after which the reproductive organ is wholly ovarian. A case recently described by Prof.

F. Braem is very suggestive. He experimented with a simple Annelid worm, *Ophryotrocha puerilis.* Taking a female which had ripe eggs and showed no trace of hermaphroditism, he divided it into two. The head portion, with thirteen segments, was isolated. In three weeks it had regenerated seven segments with parapodia. It was then killed and found to be male. The ova had mostly disappeared from the reproductive organs, leaving only a residue, and a functional testicular portion had developed, which was producing spermatozoa. Braem suggests than in consequence of the amputation the very young, indifferent germ-cells had developed into male cells, which require less subsistence than ova. What is certain is that the reproductive organs had changed from producing eggs to producing sperms, and such cases appear to us to favour the view that the sex-difference is fundamentally physiological.

In this connection Dr. F. H. A. Marshall remarks: "When once we admit the existence of latent (*i.e.* recessive) sexual characters in individuals in which the characters of one sex are dominant, and that under certain circumstances those of the latent sex can develop at the expense of the dominant ones, in response to appropriate physiological stimuli, we are compelled to acknowledge also that the sex of the future individual is not always predetermined in the gametes or even in the fertilised ovum, but may be called into being at a later stage in life." The prevalent view to-day, that sex is irrevocably determined in the germ-cells before fertilisation or in the fertilised egg-cell, seems to be true in certain cases, but it is in itself too simple. It requires physiological re-statement, and it requires the addition of a number of saving clauses.

It must be remembered that many at least of those who are keenest on the scent of morphological criteria are also alive to the importance of trying to get at the physiological realities behind these. Thus we find Prof. Wilson saying, "Since the two classes of spermatozoa differ in nuclear constitution, it is highly probable

that they differ in respect to their metabolic processes," or, again, "Upon what conditions within the fertilised egg does the sexual differentiation depend? In some way, we may now be reasonably sure, upon the physiological reactions of nucleus and protoplasm."

§ 11. *Conclusion*

In conclusion, our view is that the difference between an ovum-producer and a sperm-producer is fundamentally a difference in the balance of chemical changes, *i.e.* in the ratio of anabolic and katabolic processes, which may, of course, have its structural expression in the relation of nucleoplasm and cytoplasm. Nor do we leave this difference in metabolism-rhythm as a mere vague phrase, for we see its analogue in the contrast between the ovum and the spermatozoon (though it is quite unwarrantable to think of these as being in themselves respectively female and male cells), between the macrogamete and the microgamete, between the encysted and the flagellate cell, between the plant and the animal, and in many a familiar contrast all through the series of Organisata. We adhere, in short, to the thesis of *The Evolution of Sex*, that the sex-difference is but one expression of a fundamental alternative in variation, to be seen throughout the world of life. This view finds strong experimental confirmation in Baltzer's investigations on the plasticity of sex-conditions in Bonellia according to the nurture, in Geoffrey Smith's study of the constitutional consequences of parasitic castration in crabs, and in Riddle's work on the control of sex in pigeons.

CHAPTER XIV

SOCIAL ASPECTS OF BIOLOGICAL RESULTS

"Without heredity no amount of natural, sexual, or reproductive selection would avail to progressively change, still less to differentiate, living forms."—KARL PEARSON.

"The causes refer to our ancestors, our teachers, and the surrounding conditions of society, and with the causes must the responsibility be pushed backwards. The unhealthy parents, and not the immoral children, are responsible; the unfitted teacher, and not the misbehaving pupil, should be blamed; society, and not the criminal, is guilty. To take it in its most general meaning, the cosmical elements, with their general laws, and not we single mortals, are the fools."—MÜNSTERBERG.

§ 1. *Relations of Biology and Sociology.*
§ 2. *The Chief Value of the Sociological Appeal to Biology.*
§ 3. *Originative Factors in Evolution.*
§ 4. *Social Aspects of Heredity.*
§ 5. *Directive Factors in Evolution.*

As the general results of biological investigation must apply, *mutatis mutandis*, to man as well as to other organisms, we naturally look to Biology for some practical guidance in relation to human affairs. Thus what we have said in regard to the heritability of predispositions to disease may be of some practical utility. Similarly, the long discussion regarding the transmission of acquired characters has some practical corollaries. When all is said, however, we cannot but feel that the application of biological results is *only beginning*, and beginning with a tardiness which is a reproach to human foresight. There

can be no doubt that it would "pay" the British nation to put aside a million a year for research on eugenics, or the improvement of the human breed.

I may be permitted here to quote a notable passage from the foremost British experimenter on heredity, Mr. William Bateson (1905, p. 589):

"There are others who look to the science of heredity with a loftier aspiration; who ask, Can any of this be used to help those who come after to be better than we are—healthier, wiser, or more worthy? The answer depends on the meaning of the question. On the one hand, it is certain that a competent breeder, endowed with full powers, by the aid even of our present knowledge, could in a few generations breed out several of the morbid diatheses. As we have got rid of rabies and pleuro-pneumonia, so we could exterminate the simpler vices. Voltaire's cry, '*Écraser l'infâme,*' might well replace Archbishop Parker's Table of Forbidden Degrees, which is all the instruction Parliament has so far provided. Similarly, a race may conceivably be bred true to some physical and intellectual characters considered good. The positive side of the problem is less hopeful, but the various species of mankind offer ample material. In this sense science already suggests the way. No one, however, proposes to take it; and so long as, in our actual laws of breeding, superstition remains the guide of nations, rising ever fresh and unhurt from the assaults of knowledge, there is nothing to hope or to fear from these sciences.

"But if, as is usual, the philanthropist is seeking for some external application by which to ameliorate the course of descent, knowledge of heredity cannot help him. The answer to his question is *No*, almost without qualification. We have no experience of any means by which transmission may be made to deviate from its course; nor from the moment of fertilisation can teaching, or hygiene, or exhortation pick out the particles of evil in that zygote, or put in one particle of good.

From seeds in the same pod may come sweet peas climbing five feet high, while their own brothers lie prone upon the ground. The stick will not make the dwarf peas climb, though without it the tall can never rise. Education, sanitation, and the rest are but the giving or withholding of opportunity."

It seems to us that it may be useful to devote this chapter to an elementary discussion of the relations of Biology and Sociology, and especially to an inquiry into the bearings of biological ætiology on social problems.

Sociologists—that is to say, those who are engaged in the scientific study of the origin, development, structure, and functions of human societary forms—have admittedly a difficult task, and it is not surprising that they should look about for help on many sides. In recent years many writers on sociological subjects have appealed to biology for assistance and have used biological formulæ in their interpretations. The title of the admirable journal *Archiv für Rassen- und Gesellschafts-Biologie* is very significant. Let us try to *illustrate* at once the value and the risks of the sociological appeal to biology. Our point of view may seem very obvious to some, absurdly cautious to others; it seems to us consistent with scientific method.

§ 1. *Relations of Biology and Sociology*

Every one admits that in biology—the scientific study of the origin, development, structure, and functions of organisms as such—it is useful to appeal to physics and chemistry. Although it has not been possible, to our thinking, to translate the biological description of any vital sequence into physical and chemical terms, the methods of physical and chemical analysis have been very valuable in biological study, deepening it and broadening it, and enabling us to see more clearly what is distinctively vital, the autonomy of the organism. The utility of the analytic method has increased in proportion to

the completeness with which it has been possible to discriminate the numerous chemical and physical factors which contribute to the result which we call vital activity.

By analogy, then, it seems on *a priori* grounds legitimate to expect that biological analysis applied to the life and history of societary forms will be fruitful; and the few steady steps already taken in this direction are full of promise. But the analogy also suggests that the result of analysis in terms of lower categories will in the long run be to bring the distinctively social into stronger relief, and that certain progress in the utilisation of biological formulæ will depend on the relative completeness with which the biological factors operative in social activity can be discovered. A chemico-physical analysis of organic processes which left out electrical factors would be inept indeed; a biological analysis of social processes which left out, say, the "mutual aid" instinct would, we venture to think, be equally fallacious.

From time to time in biology some success in physico-chemical analysis has led to the fallacy which Comte called "a materialism"—the premature attempt to formulate the phenomena of a higher order of facts in terms of the categories of a lower order of facts, premature in that it attains an apparent success only by ignoring the most essential features; *e.g.* in this case, those distinctive peculiarities of self-regulation, adaptive response, and the like, which give organisms their peculiar apartness from all inanimate systems. It is impossible to argue the matter here, and it is impossible to tell what unification of descriptive formulæ may be in the lap of the future; but we are, we think, stating a matter of fact, not expressing a personal opinion, when we say that it is at present an inaccurate "materialism" to pretend that we can formulate any distinctively vital phenomenon in terms of mechanical (physico-chemical) categories. In recognising and appreciating the operation of the chemical and physical factors which contribute to the result

which we call the life of an organism, the biologist has so far simply brought the distinctively vital into greater prominence.

Similarly, in regard to the biological analysis of social sequences, there seems to us in recent literature some warrant for protesting against the "materialism" (in Comte's sense) of pretending that sociology is merely a higher department of biology, and a human societary group no more than a crowd of mammals. We have little faith in a biology which does not frankly admit that an organism is a new synthesis when compared with inanimate systems, and we have equally little in a sociology which does not consistently recognise that a human societary unit, however simple, is also a new synthesis as compared with the beasts of the field—a unity with a distinctive mode of behaviour, with a whole that is more than the sum of its parts; in short, with a life and mind of its own.

The fallacy of regarding sociology as no more than a recondite branch of biology is not merely verbal, implying differences of opinion on the tedious question of the best definitions of these two sciences; it involves a misconception of what human society is, a misconception which is discredited by the facts of history and experience. No one doubts that the life of a social group is made up of a complex of activities of individual persons; but these are integrated, harmonised, and regulated in a manner as far beyond present *biological* analysis as the integration, harmonisation, and regulation of the chemical and physical processes in the individual organism are at present beyond *mechanical* analysis.

Nor is the "materialism" a theoretical fallacy merely; it has its practical side. A cattle-breeder has been known to produce by careful selection a prize bull, almost perfect according to the physical standard aimed at, but with the serious vital defect of being sterile; so preoccupation with a purely biological ideal might, in relation to the human race, result in consequences which were anything but advantageous socially. We venture

to say this although there seems at present much more danger of the converse practical fallacy of forgetting that the biological ideal of a healthful, self-sustaining, evolving human breed is as *fundamental* as the sociological ideal of a harmoniously integrated society is *supreme*.

In any case, it is useful to recognise that the biological and the sociological ideals are not synonymous. As a matter of fact, though the former should contribute to the latter, which should include it, the practical clashing of the two ideals is familiar and interesting. Sociologically regarded, illegitimate children do not appear to be very desirable; biologically regarded, they are often very valuable assets. Sociologically regarded, it seems quite consistent with progress that the trawling industry should flourish; but, what with pleasant food on the one hand and pleasant dividends on the other, we run some risk of forgetting what the biologist deplores, the elimination of the splendid physical type of the line fisherman and the threatened disappearance of one of the manliest of callings. Scores of similar instances will occur to every one.

The danger of trying to press biological formulæ into the service of sociological interpretation is complicated by the actual history of the sciences. It is well known that the sociological inquiries of Malthus as to human population influenced Darwin, Wallace, and Spencer, and that the concept of natural selection in the struggle for existence came to biology from above rather than from within its own sphere. The same is true of the fruitful idea of division of labour, of the general idea of evolution itself, and of others—they came to biology from the human social realm.

To keep to the concept of selection for a moment: it was applied to plants and animals, it was illustrated, justified if not demonstrated, and formulated; and now with the imprimatur of biology it comes back to sociology as a great law of life. That it is so we take for granted, but it is surely evident that in social

affairs, from which it emanated as a suggestion to biology, it must be re-verified and precisely tested. Its biological form is one thing, its sociological form may be another. Perhaps it requires to be corrected by other laws of social life which have meanwhile been recognised. Perhaps there may be other hints from human social life as to the factors in evolution, whose importance we shall not recognise until they have been projected upon the world of plants and animals and verified there. In any case, a formula borrowed from another science and applied to a new order of facts—even to those in regard to which it first arose as a suggestion—must be rigorously tested. Otherwise, both organic and social sciences resolve themselves into sociomorphic illusions.

§ 2. *The Chief Value of the Sociological Appeal to Biology.*

As it seems to us, the chief value of "the Appeal to Biology" on the part of students of sociology is threefold:

(1) The analysis of biological factors operative in social sequences may serve to bring into stronger relief what is distinctively social. Thus when we analyse out what is due to natural inheritance, we see more clearly what social heredity really is. When we analyse out the various forms of natural selection operative in mankind, we see how much or how little selection there is which cannot be expressed in that formula.

(2) The biological analysis may serve to show that certain features of social life have what we may call organismal mainsprings, and become more intelligible when traced back to these. Thus the relative lack of fertility in fine human stocks requires biological as well as sociological interpretation. Again, no one can do justice to the social significance of sex or of play who does not know the biology of these. Or again, looking at this value from another side, the relatively simpler biological ideals, which must remain fundamental, *e.g.* of physical culture

and eugenics, may afford a useful touchstone for testing the validity of the more complex sociological ideals.

(3) The parallelism of the two sciences is such that biological conclusions and experiences may have great suggestive value to sociology, aiding in the discovery of sociological laws and indicating practicable possibilities of social evolution.

To illustrate this threefold value of the appeal to biology, and at the same time the risk that biology, used unduly as a support, may pierce the sociological hand, we propose in this chapter to consider a few biological generalisations and to inquire into their bearing on sociological problems.

§ 3. *Originative Factors in Evolution*

Variations.—Our biological knowledge of the nature and origin of those changes or variations which form the raw material of organic progress is still incipient; yet the little we know must be borne in mind in sociological discussions. There is general agreement that inborn variations—which give every organism its individuality—are the expression of changes in the intricate architecture of the germ-plasm. It is suggested that they are due (*a*) to the influences of the environing "body," with its variable nutritive stream, on the germ-cells; (*b*) to the intricate permutations and combinations preparatory to and implied in fertilisation; and (*c*) perhaps to what may be called growth-changes in the germ-plasm as it is continued from generation to generation. We are sure that these endogenous or germinal changes, expressing themselves in development, supply the raw material of evolution on which selection operates, and we are not sure that there is any other source of raw material.

Compared with most organisms, man is a slowly reproducing, slightly varying, creature. In so far as deeply ingrained characters are concerned, a bodily change in the race by natural

inheritance is likely to be slow. Thus we are led to look for other than germinal origins of social variations; thus we are led to suspect that when a social evolutionary process—up or down—is rapid, there must be super-organic factors at work. The distinction between organismal and social variations is obvious. The distinction between inborn variations and acquired modifications (which may be very rapidly diffused) will be alluded to later on.

While the facts seem to suggest that most of the organic variations which occur in civilised communities are simply slightly novel combinations and permutations in that complex system of ancestral contributions which we call our natural inheritance, the recent work of investigators like Bateson and De Vries has led us to recognise that discontinuous or transilient variations are of not infrequent occurrence in organisms. A "new departure," a remarkable change of organic equilibrium may suddenly appear, and may come to stay, especially if it be favoured by inbreeding or some form of isolation. It seems certain that a definite breed of cattle may arise in a single farm-yard, may be inbred until it attains dominant prepotency, and may after a while persist in its integrity in spite of occasional inter-crossing. If this be so, we can better understand how a particular human strain—such as "the Celtic type"—may be so prepotent that it persists as an important social factor in spite of much mingling of stocks. On the other hand, a genius is a transilient variation who usually does not come to stay, except as an immortal spirit embodied in literature or art.

The view that man has a range of psychical variability as large as his range of physical variability is small, does not seem to us supported by facts. The view that man's psychical variations are independent of natural inheritance is contradicted by careful investigations, such as those of Karl Pearson (1903). The useful fact to emphasise is that man, though slowly or slightly *variable*, is rapidly and exceedingly *modifiable*, and that

social organisation provides a means—an external heritage—whereby the results of modifications may be practically though not organically entailed. To this elementary distinction—necessary, however, for clear thinking—we must repeatedly refer.

By a "social variation" we mean a change in the organisation of a societary form, and it is not within the scope of this chapter to discuss its nature and origin. That is part of the task of the sociologist; and its accomplishment lies far ahead. It may not be presumptuous, however, to make this suggestion. A variation expressing itself in an individual organism is marked by changes in many individual units, and these changes have to be described and measured. But the origin of the variation was germinal, in the "immortal" germ-plasm which gives continuity to the chain of transient generations. Thus we are led to think that those social changes that really count must have their basis in that which is to societary forms what the germ-plasm is to generations of organisms, the *esprit de corps* (in the unrealisable full meaning of the phrase!) which gives unity to every societary form whether it be big or little.

Modifications.—Besides "variations" in the strict sense, there are other organic changes, technically known as "modifications," or, more awkwardly, as "acquired characters." They are definable as bodily structural changes acquired by the individual organism as the direct result of changes in function (use or disuse) or of changes in the environment, and so transcending the limits of organic elasticity that they may persist after the inducing conditions have ceased to operate. They are exogenous, somatogenic changes, as contrasted with endogenous, blastogenic changes. They are the direct results of peculiarities in "nurture," as contrasted with inborn changes in the inherited "nature," to use the convenient words with which Mr. Galton, following Shakespeare, has made us familiar. That they are, after all, reactions of the inherited nature to

new conditions of stimulus, both positive and negative, is obvious. Now, the important point is that we cannot with any certainty count these "modifications" as part of the raw material of evolution (progressive or retrogressive), for we have no good evidence to show that they can be hereditarily entailed as such, or even in any representative degree transmitted to the offspring.

It is admitted that some deeply-saturating modifications may, by affecting the nutritive stream, indirectly affect the germ-plasm, but there is no proof of the transmission of any modification as such. The evidence for this assertion will be found, for instance, in preceding chapters.

It is admitted that the organism—notably the human organism—is often extraordinarily modifiable, and that similar conditions may induce similar modifications on generation after generation, so that an appearance of heritability results.

Moreover, as Professors Mark Baldwin, Lloyd Morgan, and H. F. Osborn have pointed out, modifications that are effectively advantageous—adaptive responses, in fact—may have an indirect evolutionary importance, for they may serve as sheltering, life-preserving, or welfare-furthering screens until coincident endogenous variations in the same direction have time and opportunity to establish themselves. Thus a modificational change may be gradually replaced by a strictly variational, and, by hypothesis, heritable one. Then the screen or veneer may be done without.

If the conclusion of the majority of biologists be correct, that modifications are not as such transmitted, there are some obvious sociological corollaries. We have, in the progress of education, therapeutics, and hygiene, unceasingly striking evidence that the human organism is very plastic; but we cannot delude ourselves with the belief that its precise gains or losses are ever as such transmitted. Therefore, it has to be our practical endeavour that advantageous modifications be

re-impressed on each successive generation, and that detrimental modifications be avoided.

But the biological conclusion has to be in an important respect corrected for the social realm, in view of the fact that man has an external heritage of custom and tradition, institution and legislation, literature and art, which is but slightly or not at all represented in the animal world, which yet may be so effective that its results come almost to the same thing as if acquired characters were transmitted. They are re-impressed on the bodies and minds of successive generations, though never ingrained in the germ-plasm. It seems probable that not a few of the biologically and socially unfit are only *modificationally* veneered, or repressed, or arrested.

Moreover, while among plants and animals the organism is often largely a creature of circumstances, very thoroughly in the grip of its surroundings and mastered by them, it becomes otherwise as we ascend the scale of being. Increasingly we find the organism—be it bird or mammal or man—much more master of its fate, able to select its own environment in some measure, able to modify its surroundings as well as be modified by them. As we take a bird's-eye view of the course of evolution, must we not recognise the gradual emergence of the free agent—the operation of what has been badly called "organic selection"?

§ 4. *Social Aspects of Heredity*

We have defined heredity as the genetic relation between successive generations, and inheritance as all that the organism is or has to start with in virtue of its hereditary relation to parents and ancestors. All sociological talk that appeals to a "principle," "law," or "force" of heredity should be ruled out of court.

The hereditary relation is sustained by the germinal material, and the precise study of this physical basis has done much of

recent years to define the way in which generation is linked to generation. The fundamental fact of the continuity of the germinal material from generation to generation—the fact which is in biology like the first law of motion in physics—secures that persistence and continuity of organic kinship on which the possibility of a society depends. The peculiar way in which the germ-plasm accumulates within itself what we must regard as multiple sets of hereditary contributions, and becomes like a mosaic, or like capital growing at compound interest, is a fundamental fact for sociologist as well as for biologist. It is the organic condition of the social instinct.

The great generalisation known as Galton's Law of Ancestral Inheritance, according to which inheritances are on an average made up of a half from the two parents, a quarter from the four grandparents, an eighth from the great-grandparents, and so on, may require some adjustment as regards the precise fractions, and in relation to cases of inter-crossing, but the general fact seems to have been well established, and it is eloquent. Taking it along with Professor Karl Pearson's evidence that the inheritance of psychical characters can be formulated like that of physical characters, we are in a better position to understand what is called "social solidarity" and "social inertia." We are able to realise more vividly how the past has a living hand on and in the present, even to feel, perhaps, that there is a danger of fallacy in insisting too much on either past or future when we have to deal with the continuous stream of life. Mr. Galton's generalisation makes reversions, survivals, recapitulations, and the like more intelligible.

Very suggestive also is Mr. Galton's elucidation of Filial Regression—that there is a continual and necessary tendency to approximate to the mean of any stock. In proportion as two parents are divergent from the mean of their stock, will be the succession-tax levied upon their offspring, which will tend to approximate, up or down, towards the general level. This,

is capable of statistical proof, and it follows from the broad fact that each parental contribution is a mosaic of inheritance, which, except in cases of very careful selection (for good or ill), must eventually be traced to a crowd of ancestors representing the average mediocrity of the stock.

Thus we have light thrown on the familiar facts that children of exceptionally gifted pairs are often commonplace, and that children of worse than commonplace parents are often very fair samples of the breed. More generally, we see, as Mr. Galton says, that there is a general and inevitable levelling-up and levelling-down, that a society biologically considered tends to move like a great fraternity. Just as the "Hereditary Genius" studies of Mr. Galton gave us a biological basis for pride of race and a respect for true aristocracy, so his Filial Regression formula is a message to democracy.

The facts of inheritance acquire profound sociological significance when we inquire into the relative rates of fertility in different sections of a population, and into the probabilities of the production of highly endowed types in these different sections. It seems to us that one of the most suggestive of biological contributions to sociology is that famous "Huxley Lecture" in which Mr. Galton indicated some of the probable practical corollaries of his statistical laws.

Man is a slowly varying organism, and he is peculiarly liable to have his inborn nature concealed by a veneer due to nurture; but there is no ignoring the fact that there are great differences in quality and quantity of hereditary endowment. As was long ago expressed in immortal parable, there are those who have ten talents, those who have five, and those who have only one.

Now, the differences in hereditary endowment—of strength or intelligence, of stature or longevity, of fertility or social disposition, have a certain regularity of distribution, so far as we can measure them at all. They conform to what is called the Normal Law of Frequency, which is always illustrated when

variations are due to the combined action of many small and different causes. Human variations, whether bodily or mental, may be registered on a curve of frequency, just like the variations of poppies or jelly-fishes—on the same sort of curve as may be illustrated by plotting out the marks round the bull's-eye in target practice, or the numbers which come to the top in so many thousand throws of the dice, or the marks in a competitive examination with a large number of candidates.

Let us briefly recall Mr. Galton's argument. If we take a precisely measurable quality like stature, we find that the average height of a large number of adult Britons is 5 feet 8 inches; above this line of mediocrity (R) there are taller men who may be arranged in groups, the means of which are separated from one another, by 1¾ inches; we may call these +S, +T, +U, +V, +W, and +X, till we end in giants of 6 feet 6 inches; we may give to the distance between the groups (1¾ inches) the name "normal talent." Thus while the average adult has 39 "normal talents" of stature (5 feet 8 inches), the six groups above him, rapidly decreasing in numerical strength as we ascend, have respectively 1—6 talents more than mediocrity.

On the other side of mediocrity, there are of course groups of minus variations, groups which we may call −s, −t, −u, −v, −w, and −x, with 1—6 talents fewer than the normal equipment of 39; and the minus or left side of the curve exactly reflects the plus or right side. A giant of 6 feet 6 inches would belong to the small and very select sixth class above mediocrity (+X), while a dwarf of 4 feet 10 inches would belong to the sixth class below par (−x); and there are apparently as many of the one as of the other. Mr. Galton maintains that the curve holds good for any particular measurable quality taken separately, and that it also holds good when the qualities are grouped. "It can be employed to give a general idea of the distribution of civilisation, in so far as it is normally distributed . . . and the same for any group of normal qualities."

The next step in the argument is important and brings us into closer touch with social problems. Mr. Charles Booth, in his well-known demographic studies, has arranged the population of East London into grades of "civic worth," beginning with criminals, semi-criminals, and loafers, going on with increasing numbers to casual workers, intermittent workers, and thence to regular earners under *22s.* a week, and so on. The results show "a fair approximation to the normal law of frequency." Again we have the groups, +S, +T, +U, etc., and the groups, −s, −t, −u, etc., forming the two sides of an approximately similar and symmetrical curve.

It is easy to say that one knows of this, that, and the other one who rose into class +T by sheer luck; and of this, that, and the other one who fell into class −t by the hand of God—a fire, a wreck, an explosion, and what not; but when we are dealing with large numbers, it does not seem that these exceptional exaltations and depressions of individuals are of vital moment. It is also evident that the standard of civic worth used by Booth is only one of many standards—that of economic production under present conditions—but to begin with we must measure by one standard at a time. We know that it would be individually unjust to put, say, Arnold's "scholar gipsy" on the minus side as a casual worker, but there are not many scholar gipsies.

The next step in Mr. Galton's argument might be described as a financial valuation of babies. Suppose we could import at the present moment ten legions of boys of sound physique and scouting intelligence, not crammed with intellectual fat like Strasburg geese with the physical analogue, but alert in understanding of methods and with unchecked inquisitiveness, what great national gain it would mean! It would be a good investment, and it is within reach every year, since far more than ten legions of this type of boy are being born annually in our midst. That they do not effect all they might do, is partly

because of mis-education, but also because there is a simultaneous appearance of an enormously greater number of boys who are emphatically *not* of this type.

Dr. Farr, the eminent statistician, tried to estimate the social money-worth of the average baby born to an Essex labourer, supposing him to live as long as and after the manner of his class. Allowing for cost of maintenance during the two helpless periods of infancy and senile infirmity, Dr. Farr came to the conclusion that the national value of the baby was about £5. If £50 be nearer the mark, it does not affect the argument.

"On a similar principle," Mr. Galton says, "the worth of a +X-class baby would be reckoned in thousands of pounds. Some such 'talented' folk fail, but most succeed, and may succeed greatly. They found industries, establish vast undertakings, increase the wealth of multitudes, and amass large fortunes for themselves. Others," he continues, "whether they be rich or poor, are the guides and lights of the nation, raising its tone, enlightening its difficulties, and improving its ideals. The great gain that England received through the immigration of the Huguenots would be insignificant to what she would derive from an annual addition of a few hundred children of the classes +W and +X."

Now, however, comes the crux of the whole argument. By a method expounded in his "Natural Inheritance," Mr. Galton has endeavoured to express in a standard table precisely how each generation of a classified population is derived from its predecessors. Keeping to the terminology that the groups above mediocrity are +S, +T, +U, +V, +W, +X, let us inquire with Galton into the origin of 35 male members of the very excellent grade +V (fourth above mediocrity, 1 in 300). (That these are not *mainly* due to marriages of + V-class parents is probably suggested by our everyday experience, and this observational conclusion is borne out by the statistics, which, in regard to some qualities, such as stature, can be made

very precise.) Mr. Galton's result is that of the 35 +V youths, six come from +V (fourth) parentages; ten from +U (third); ten from +T (second); five from +S (first); three from R, and *none* from below R.

But along with this very suggestive result, we have to consider the numerical strengths of the contributing parentages. When this is done, "we see that the lower classes make their scores owing to their quantity and not to their quality; for while 35 +V-class parents suffice to produce six sons of the +V-class, it takes 2,500 R-class fathers to produce three of them." Thus from the point of view of eugenics, if we wish to increase the number of +V-class offspring, the most profitable source is to be found among the more prepotent +V-class parents; they are three times more profitable than those of the next class, +U, and 143 times more profitable than those of class R!

Other Facts of Heredity.—One is tempted to linger over that mode of inheritance which is called true reversion, where ancestral characters that have lain latent for several generations suddenly find opportunity to reassert themselves. It is true that "reversion" has been a convenient "free toom" into which much rubbish has been shot. It is true that reversion has been terribly confused with arrests of development (usually of modificational origin), with the not uncommon variations in those numerous vestigial structures of which our body is a walking museum, with independent variations that "happen to hit an old mark in aiming at a new one" or simply suggest to the credulous a harking-back to a more or less hypothetical ancestral type, and even with the normal and everyday occurrence of filial regression. Yet it is undeniable that ancestral traits may remain long latent, apparently but never really lost, and that, in the intricate shuffling of the cards which is associated with the maturation and fertilisation of the germ-cells, they may suddenly find their appropriate liberating stimulus, and assert themselves once more.

A shepherd's cottage garden was swallowed up in a deer-forest and became a garden full of weeds; generations passed and it was once more delved; the long dormant seeds were reawakened and many old-fashioned flowers saw the light. So there may be a reawakening of almost forgotten flowers and weeds in that garden which we call our inheritance. Thus we interpret biologically what we cannot ignore in the body politic, the emergence of the old-fashioned type whom we—foxes without tails—think to dispose of under the label "reactionary"; of the restless type "neither to haud nor bind," who may be a Moses with reawakened nomad instincts capable of leading a people through the desert to a new Promised Land; or, as is often the case, of the recrudescent vicious type, who, if he cannot be pardoned when we know all, can at least be the better dealt with the better he is understood.

Another aspect of heredity has an obvious sociological significance, the dark and intricate business of hybridisation or cross-breeding, in regard to which biologists are beginning to see some daylight. If we call mankind a species, we must admit that there are many sub-species or "elementary species," and that within these again there are minor groups of more or less well-marked stocks, and that there are also somewhat divergent groups or varieties. As in the past, so still there is no small amount of exogamy or cross-breeding, and it is much to be desired that the whole matter should be carefully investigated. How far is it true that cross-breeding provokes an "epidemic of variations," that it tends to induce "reversions," that the older stock is prepotent over the younger, and so on? According to De Vries it is very generally true of plants, that a retrogressive variety (*i.e.* one different from the parent species in the marked absence of some character) will, if crossed by a typical member of the species, produce offspring which return to the original type. Is there any analogue of this "false atavism or vicinism" in human kind?

One is tempted to speculate as to the possible sociological interest of Mendel's Law, if it should be found to obtain in the minglings of human races, but as yet we have not a sufficient basis of fact. As we have seen, the inbreeding of *hybrids* of peas, stocks, mice, etc., is followed by a splitting of the offspring into true-breeding types like the two parents of the hybrids. We may suggest that careful inquiry should be made as to the results of inter-marriage among Eurasians, for if Mendel's Law holds, there should be a sifting out of pure Asiatics and pure Europeans, both probably more desirable than Eurasians, fine mentally and physically as these often are.

There are still some who find satisfaction in pointing out that as human evolution is *par excellence* a psychical evolution, biological conclusions on the question of inheritance are irrelevant, since they are based on the study of measurable physical qualities. But those who would press this point must deal with Professor Karl Pearson's "Huxley Lecture" for 1903, "On the Inheritance of the Mental and Moral Characters in Man, and its Comparison with the Inheritance of the Physical Characters" (*Journ. Anthropological Institute*, xxxii. pp. 179–237). His method was to obtain for upwards of one thousand families impartial data as to *fraternal* resemblance in physical and psychical characters in school-children. His argument was, "If fraternal resemblance for the moral and mental characters be less than, equal to, or greater than fraternal resemblance for the physical characters, we may surely argue that parental inheritance for the former set of characters is less than, equal to, or greater than that for the latter set of characters." His conclusion, after many years of investigation, was that "the degree of resemblance of the physical and mental characters of children is one and the same," or, more concretely, "we inherit our parents' tempers, our parents' conscientiousness, shyness, and ability as we inherit their stature, forearm, and span." The psychical characters are

inherited in the same way, and at the same rate as the physical.

But one of the general points of this chapter may be illustrated here. In proportion as we succeed in analysing out the biological factors in our Natural Inheritance shall we see clearly what is meant by "Social Heredity." What do we mean by it? Not merely that facts of family and stock inheritance may have great social importance, whether they concern the history of a dynasty or the physical deterioration of a proletariat; not merely that great biological generalisations, such as Filial Regression, or the inverse ratio between rate of reproduction and degree of individuation, have direct sociological relevancy; not merely that there are probably obscure laws of periodic recurrence, such as "the law of generations"; we mean especially that complex process by which much of what is most precious to us appears to be sustained from generation to generation in a *social heritage*, by tradition, conventions, institutions, laws, and the whole framework of society itself. It is here that the biologist leaves off, and the sociologist must come in.

§ 5. *Directive Factors in Evolution*

Selection.—Passing now to the *directive* factors in evolution in contrast to those which are originative and conservative, we find practical unanimity in recognising the importance of *selective processes*. We use a plural phrase in protest against the persistent fallacy of taking a narrow and crude view of what occurs in many different modes, at many different levels, and with very varied degrees of intensity.

Variety of Modes, Levels, and Intensity in Selective Processes.—As Darwin clearly indicated, the phrase "struggle for existence" is to be taken in a wide and metaphorical sense. In point of fact, it is in operation whenever and wherever the degree of effectiveness of vital response is of critical moment,

not merely in helping *survival* at the time, but in strengthening foothold, increasing comfort, lengthening life, promoting reproductive success, and so on.

It may be a miserable squabble around the platter of subsistence, but it may be a gentle endeavour after well-being. It may be prompted by "love" as well as by "hunger," using both words in the widest sense; it may be other-regarding as well as self-preservative.

There may be struggle between foes of quite different natures, *e.g.* birds of prey and vermin; competition between fellows of the same kin, *e.g.* brown rat against black rat; opposition between the sexes (cf. courtship of spiders, in which the female often devours the male, and human competition between male and female doctors, clerks, etc.); self-assertion against the quite indifferent, often merciless "weather" of the physical environment. The phases of "struggle" are as varied as life itself.

Interference with Natural Selection.—Not a few sociological writers have echoed the warning of Herbert Spencer that modern hygienic and therapeutic methods interfere with the natural elimination of the weaklings whose survival consequently becomes a drag on the race, and there is doubtless some force in the argument, especially if we could confine ourselves to an entirely biological outlook. It appears to us, however, that the practical corollary that we should cease from interfering with natural selection, as the phrase goes, is as fallacious as it is impossible. (1) It seems a little absurd to speak of, say, the prevention of an artificially exaggerated infantile mortality as if it were an interference with the order of nature. (2) Much weakness which may readily become fatal is simply modificational, due perhaps to lack of nutrition at a critical moment; many weakly children grow up thoroughly sound; and even if we do keep alive some whose constitutions are intrinsically bad, we are at the same time saving and strengthening many whose intrinsically good constitutions only require temporary shelter.

One enthusiast over microbic selection says: "The higher the infantile death-rate which medicine so energetically combats, the surer is the next generation of being purged of all weakly and sickly organisms." But he omits to record the fact that the infantile maladies also affect the intrinsically strong and capable, and often weaken them, one might say, quite gratuitously. (3) Many of the microbic agents which thin our ranks are very indiscriminate in their selection, and even if we believed that in warring against microbes we are eliminating the eliminators who have made our race what it is—as the enthusiastic apologists for Bacteria declare—it is surely open to us to put other modes of selection into operation. It were a sad confession of incapacity if man could not select better than bacteria. (4) Finally, since we cannot keep to the biological outlook, is it ridiculously old-fashioned to plead that even when the physical constitution is miserable, the weakling may be a national asset worth saving, for its mental endowment, for instance, and for other reasons? *That the weakling is to be allowed to breed more weaklings if it can, is another matter.* Every one agrees that the reproduction of weaklings should be discouraged in every feasible way—in every way compatible with rational social sentiment.

Multiplication of the Unfit.—We have to face a more difficult problem when we consider the multiplication of the relatively unfit. It is, we suppose, true that these have now a better chance to survive and multiply than at any other epoch in the history of our race. Especially perhaps in Britain do the weeds tend to increase more rapidly than the flowers. It is impossible to ignore the seriousness of the outlook. If, as Professor Karl Pearson points out, 25 per cent. of the married couples in Britain produce 50 per cent. of the next generation, how much depends on the character of that 25 per cent. From the most diverse regions we have reports of the alarming increase of what not even the most optimistic can regard as other than undesirables. In a fine climate and in a period of cheap food

and high wages, the ratio of defectives—including deaf and dumb, lunatics, epileptics, paralytics, crippled and deformed, debilitated and infirm—is said to have increased from 5·4 per 1,000 above 15 years in 1874 to 11·6 in 1896. Particular statistics, such as these, may be open to criticisms, but there are scores of similar statistics from almost every civilised country, and there is no escape from the general result. As Emerson said, we are breeding men with too much guano in their composition.

A Host of Practical Suggestions.—Needless to say, many of the inquirers who have become impressed by the facts have not been backward in making practical suggestions, which might be arranged, if one had time, on an inclined plane. Some, more trustful in natural selection than in any human device, have taken up an extreme *laissez-faire* position, which, as human society is constituted, is quite untenable. The other day we passed by a rock village in Italy which was not so long ago in the direst sense *left to itself* when cholera broke out within it, sealed up, as it were, like a bee-hive diseased—but it is idle to talk of leaving natural selection free play in any civilised community. Others, going to the opposite extreme, have advocated what may be called surgical methods for both sexes to a degree that is more than spartan. Between these extremes we find all manner of suggestions. We need only refer to the marriage examination and certificate system which is being increasingly discussed—to much profit, it seems to us—in Germany; the segregation schemes which suggest that those obviously unfit who have to fall back on the State (*i.e.* the relatively fit citizens) for support should forfeit the right to reproduce, for which, again, there is much to be said; and the wise and gentle constructive eugenic proposals with which Mr. Galton has made us all familiar.

Probably every one who is at all aware of the facts will admit the desirability of giving attention to eugenics or the improvement of the human breed, positively, if possible, in the way of

increasing the numbers of the effective, or negatively, in the way of trying to reduce the multiplication of the unfit. Inquiry into these subjects is comparatively new, discussion of them is still rare, a superstitious attitude towards them is still very common—we cannot tell what may come about when a conscience relative to these things is developed, or in the wake of great social changes.

Meanwhile, convinced as we are as to the hopefulness of various forms of eugenic selection, we cannot but enter a protest against the impetuous recommendations of some who suggest methods of surgical elimination to an extent that is almost grotesque.

We would suggest the following cautions:

(1) We are far from being omniscient in regard to variations. Some deteriorative changes are well known, and history has given its verdict against them. There are surely few who would encourage the marriage of those suffering from syphilis, marked tuberculosis, senility, diabetes, deaf-mutism, chronic nephritis, hæmophilia, organic heart-disease, contracted pelvis, and the like, Every one agrees that there should be no breeding from epileptics, paralytics, lunatics, and so on, but many other variations are unknown quantities. The unpromising bud may burst into a fair flower. Virchow's thesis of the pathological origin of some variations is not to be lightly brushed aside. There is an optimism of pathology. No one would propose to *encourage* the breeding of doubtful variants on the off-chance of an occasional genius, but the race owes much to weaklings none the less. A man belonging to a family which has been manufacturing cystin for three generations should not have children—he would not pass the German marriage examination —but in himself he may be a very valuable national asset. Some of the lists given by the social surgeons are quaint in their unpracticality; thus one includes "a criminal taint"— as if that were a rarity, or as detectable as deaf-mutism—and another includes "pauperism."

(2) Is there not much to be said in support of the view that many of the unfit are only *modificationally* unfit—simply ill-nourished plants in the crowded garden? Are we not apt to underrate the plasticity of human nature and the ready repressibility of hereditary items? Is there strictly speaking such a thing as a transmissible disease, apart from pre-natal infection? Is not a predisposition to disease the most that is transmitted? Are not many criminals mere anachronisms?—people out of time or out of place, who require not incarceration or worse, but only transplanting. Records of Jukes' families, or of the woman whose 709 descendants cost the state a quarter of a million are impressive, but one has to remember the modificational effect of social ostracism. One can hardly doubt that the high rate of criminals among illegitimate children—said to form one-tenth of the births in Germany—is artificially created. In passing we may note, as of interest, the formation of a League in Germany to protect not merely illegitimates, but their mothers.

(3) While it is undoubtedly true that strongly developed evil characters may have a great power of persistence even beyond the third and fourth generation, just as strongly developed good characters may have, is there not a tendency to exaggerate the consequent tainting of stock? Dr. Archdall Reid has expounded the tendency of the uncontrolled alcoholic type to work itself out, and the same is true of other types. If germinal selection expresses a reality, we should expect taints to be swamped, just as excellences often are.

(4) There is no doubt that Mendelian phenomena of inheritance occur in man, therefore we should be slow to say that it is not possible to bring a clean thing out of an unclean. When an immune wheat plant and a non-immune are crossed, the resulting hybrids are all susceptible to rust. When these are self-fertilised, *i.e.* inbred, they produce seed from which appear "rusty" plants and immune plants in the ratio of 3 : 1. It

may be that there are *analogous* phenomena awaiting discovery in the case of man.

Our general position is that among civilised men the sentiments of solidarity and sympathy are too precious and too strong to admit of *much* social surgery, or of the more thoroughgoing methods of reproductive elimination, which moreover assume the possession of more science than is really available. On the other hand, there seems much to be said for restricting the reproduction of undesirables who fall back on the State for support, for some sort of marriage-tests, for developing a social prejudice against reproduction among the victims of markedly bad inheritance, for a fuller and deeper recognition of woman's rights both as to mating and maternity, for eugenic devices such as Mr. Galton has suggested, and so on. But there is one other suggestion we wish to try to express.

Militarism.—In his luminous book, "Evolution and the War," Dr. Chalmers Mitchell has shown the fallaciousness of comparing modern warfare with anything that goes on in nature. Thus, "Modern nations are not units of the same order as the units of the animal and vegetable kingdom." . . . "The struggle for existence as propounded by Charles Darwin, and as it can be followed in nature, has no resemblance with human warfare."

If a comparison between human warfare and "the struggle for existence in nature" be insisted on, it will have to be admitted that *biologically regarded* even a righteous war is a reversion to the crudest mode of struggle, a recourse in great part to the physical force test—an attempt to transcend which surely marks the transition from barbarism to civilisation. It is agreed, of course, that, *socially regarded*, a righteous war may be a discipline in nobility.

Man is not shut up to imitate this or that particular mode of the struggle for existence whch he sees in nature, which indeed includes co-operative integration as well as internecine conflict. If he indulges in or is forced to modern human war-

fare, he must expect dysgenic consequences. If he presses the biological analogy in protest and justification, he has to be reminded that there is no biological warrant for supposing that victory *must* imply a survival of the fittest as judged by our human standard of value. Among the dysgenic consequences to be dreaded we have to think of the possible impoverishment of the race by the loss of large numbers of fine types throughout the whole population year after year (a loss mitigated in various ways, *e.g.* by the relatively slight elimination among the mothers in the stronger nationalities), of the certain impoverishment of the race by the loss of unique individualities of great promise whom we know not how to replace, and of the great risk of reversionary slipping down the steep ladder of evolution on the part of non-combatants and combatants alike, *e.g.* by the disruption of integrating idea-systems and by the frequently deteriorative influences of unexampled stress and strain.

When we contemplate any national danger we may interpret the facts *biologically*, as an American zoologist, Professor D. S. Jordan,* has recently done, in terms of the reversed selection which tends to spoil the human harvest; or *psychologically*, in terms of the changed ideas and ideals of the average man; or *sociologically*, in terms of variations in the organisation of the societary form ; but, fundamentally, these interpretations must be capable of a unification, and this it is particularly the task of the sociologist to work out. Preoccupation with the biological outlook—the breeder's point of view—will undoubtedly lead to fallacy upon fallacy, to the "materialisms" to which we have already referred ; on the other hand, an ignoring of the biological point of view means a deliberate rejection of the order of facts which we can most precisely measure and test. Moreover, the commonplace is apt to be forgotten, that when changed ideas and ideals find physical embodiment in flesh and blood, they

* See "The Human Harvest" (American Philosophical Society, April 1906 ; also separately, Boston, 1907, pp. 122).

acquire, *ipso facto*, an inertia which no belated conversion on the psychical plane can ever do away with. Not less true, however, is it that sifting, informing, and ennobling of our idea-systems will react on everyday practice and endeavour, for ideas have hands and feet. What every one must agree on is the imperativeness of strenuous effort on every plane—biological, psychological, and social—to counteract the evil crop that always springs from the sowing of dragons' teeth.

Relative Infertility of more Individuated Stocks.—Let us briefly refer to the other aspect of the fertility problem. The biologist accustomed to interpret great results in terms of selection and isolation acting on germinal variations, is not likely to be lacking in faith in what may be accomplished by attention to eugenics. But he finds it difficult to dispel the shadow cast by the fact of the relatively great infertility of what we believe to be types and stocks of high social efficiency. Over and over again, in the history of mankind, elect castes—true aristocracies—have arisen, only to disappear again in sterility, or in the course of inter-societary struggle. Even if the latter doom be averted by more evolved social organisation and racial pacification, how are we to face the fact of the dwindling fertility of what we believe to be the better stocks? It may be that the relatively recent diminution of the birth-rate among skilled workmen and the like is partly modificational or artificial, an adaptation to altered social conditions; but what can we say of the generally low fertility of the most individuated stocks?

The factors which make towards this result are probably manifold. There are probably, as Spencer maintained, automatically working physiological and psychical factors which lessen reproductivity as individuation increases. It may be that hyper-nutrition, sexual vice, the frequent absence of love marriages, operate in the same direction; it seems difficult to doubt that selfish celibacy and selfish non-maternity are in part to blame; and there are all sorts of possible factors down

to the marriages of heiresses who are often the sole survivors of a dwindling family. Dr. Ireland points to the significant fact that some of the high castes of India (Brahmins and Rajputs) who are most exclusive in their marriages do not show the usual dwindling tendency, which may be correlated with the circumstance that they are mostly poor and abstemious.

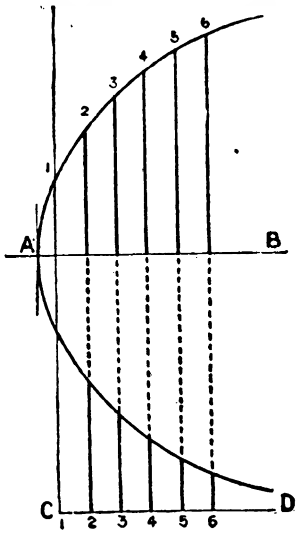

FIG. 47. DIAGRAM ILLUSTRATING THE RELATION BETWEEN REPRODUCTION AND INDIVIDUATION (from "Evolution of Sex")

Let the perpendiculars above the line A B denote the increasing degree of total individuation of a series of forms 1, 2, 3, 4, 5, 6 (say Worm, Fish, Frog, Bird, Man, Elephant). Similarly, let the perpendiculars from the line C D represent the rate of multiplication of the same forms. The curves joining the apices of the two sets of perpendiculars indicate, by their inverted symmetry, the inverse ratio of individuation and rate of multiplication.

Is there any consolation in the thought that quality is always safe against quantity, that eagles need never fear the frogs who spawn, that an inheritance may persist socially even when a lineage becomes extinct biologically? Is there any warrant for supposing that the race can continue producing from new soil crop after crop of highly individuated types, each in its turn destined to die out as a penalty for its own efficiency?

Is there any truth in the inference that failure in reproductive power is an expression of nature's verdict against dis-social isolation of privileged classes, against every self-contradictory denial of the solidarity of the social organism? In any case, is there not need for getting rid of a prudery of selfishness which keeps some of the fitter types from recognising that they have another contribution to make to the race besides their work?

It should be borne in mind that precise thinking on the subject of fertility is uncommon, that there is no general awareness that the disproportionateness of our dwindling birth-rate suggestive of disaster, and that very few have what may be called an awakened conscience on the subject. The most common-sense precautions are quite disregarded. Falling in love is out of fashion, and almost non-mammalian types grow commoner. In a sense, though it is a pity, it may be just as well that they should die out. And who, for instance, ever thinks of the wise Frenchman's saying, "My father was a farmer, I am a Professor, my son must be a farmer again"? But, apart from the slow diffusion of an interest in eugenics, perhaps the most promiseful line of activity is that of trying to promote social (including of course ethical) variations which may bring about more wholesome biological conditions.

Isolation.—The only other directive evolution-factor that biologists are at all agreed about besides selection, is isolation—a general term for all the varied ways in which the radius of possible inter-crossing is narrowed. As expounded by Wagner, Weismann, Romanes, Gulick, and others, isolation takes many forms—spatial, structural, habitudinal, and psychical—and it has various results.

It tends to the segregation of species into sub-species, it makes it easier for new variations to establish themselves, it promotes prepotency, or what the breeders call "transmitting power," it fixes characters. One of the most successful breeds of cattle (Polled Angus) seems to have had its source in one

farm-steading, its early history is one of close inbreeding, its prepotency is remarkable, its success from man's point of view has been great. It is difficult to get secure data as to the results of isolation in nature, but Gulick's recent volume on the subject abounds in concrete illustrations, and we seem warranted in believing that conditions of isolation have been and are of frequent occurrence.

Reibmayr has collected from human history a wealth of illustrations of various forms of isolation, and there seems much to be said for his thesis that the establishment of a successful race or stock requires the alternation of periods of inbreeding (endogamy) in which characters are fixed, and periods of out-breeding (exogamy) in which, by the introduction of fresh blood, new variations are promoted. Perhaps the Jews may serve to illustrate the influence of isolation in promoting stability of type and prepotency; perhaps the Americans may serve to illustrate the variability which a mixture of different stocks tends to bring about. In historical inquiry into the difficult problem of the origin of distinct races, it seems legitimate to think of periods of "mutation"—of discontinuous sporting—which led to numerous offshoots from the main stock, of the migration of these variants into new environments where in relative isolation they become prepotent and stable.

Conclusion.—Our general position is that when we pass from organisms to human societies, the whole venue changes so much that we have to be very careful in our application of biological formulæ. (1) Thus, in regard to processes of selection, we have to recognise the intervention of rational selection as an accelerant or as a brake on natural selection. (2) When a society deliberately sets to work to select discriminately among the individualties which make up its own body politic, we have to do with an infinitely subtler process than that observed when a breeder selects in his stock, or when the physical environment elimi'ates the ill-adapted members of a race. (3) There is in

human affairs a much more prominent occurrence of inter-group, inter-societary, or inter-racial selection, which introduces fresh complexities, *e.g.* that in the conflict of races the apparent victors are sometimes, in some measure, conquered by the vanquished.

In all selectionist proposals we have to face the difficulty of agreeing what we are to select for. If selection processes are to succeed, they must be consistent. As to the negative ideal of trying to lessen the precipitate of undoubted incapables, all will agree; but the positive ideal of working towards evolution is necessarily vague, meaning different things to different people. It will be generally admitted, however, that if we are to avoid fallacious endeavour, our ideal must include "eutopias" and "eutechnics" as well as "eugenics," and that it must be not merely biological but distinctively sociological in its outlook.

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